Wolf Predation on Bison in Wood Buffalo National Park

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CANADIAN WILDLIFE SERVICE

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ABSTRACT

The relationship between bison and wolves in Wood Buffalo National Park was investigated during the years 1978 to 1981. Radiolocations of 43 wolves provided information on population estimates, home range sizes, pack sizes, territoriality, dispersal, movements, and predator-prey interactions. Information obtained was supplemented with survey records from 1971 to 1981. Aerial observations indicated that wolf numbers north of the Peace River were stable from 1972 to 1977, but numbers decreased south of the Peace River during this period. There was a precipitous decline in wolf numbers in the delta from 1974 to 1975. Increased trapping may have accounted for a portion of this decline. During 1978 to 1981, human caused mortality of wolves (trapping, snaring) was light to moderate. The role of disease in controlling wolf numbers is unknown. Seven of the 43 wolves captured showed sign of mange, but there was no evidence that this disease resulted in wolf mortality.

Mean pack sizes, obtained from routine surveys during 1970 to 1981, ranged from a high of 14.5 in 1973/74 to a low of 6.0 animals in 1975/76 and 1978/79. The percentage of single/pairs ranged from a low of 6% in 1971/72 to a high of 53% in 1975/76. Large pack sizes preceded the major spring flood in 1974; flooding, disturbance and trapping in the Peace delta may have disrupted pack structure and reduced pack sizes.

Territory sizes of wolves in Wood Buffalo National Park were large. The composite territory of one pack over a three year period was close to 3000 km^2, though the annual area covered was around 1000 km^2 in size. Most frequently used areas by resident packs were considerably smaller than the general area occupied. Pack members generally formed more cohesive

units in winter, at a time when mating activity (mid-February) and den construction (mid-March) occurred. However, temporary splitting and reforming of packs during winter was common. In summer pack members were more dispersed, often separated by as much as 35 km on any one day. The average same day distance between pack members during summer was 7.9 and 14.5 km for two packs, respectively.

Wolves shifted centers of activities within their home range from winter to summer (mean distance 12.8 km), probably in response to seasonal shifts in food resources. Annual activities within territories indicated strong preference for some areas over others; wolves preferred open prairie, which comprised prime winter habitat for bison, over forested areas. Overlap in areas used by different packs was evident. In some instances, wolves which trespassed into adjacent territories were killed by the resident pack.

Winter conditions were important in affecting activity patterns of wolf packs. Travel distances by wolves decreased from early to late winter. In milder winters, wolves traveled less and killed more frequently than in more severe winters. Average distance between kills was 57.5 km. Predation of one pack was most common in the center of the territory.

A good portion (up to 50%) of wolf activity in winter was spent in close association with bison. We documented a total of 143 wolf/bison interactions. Sequences of encounters ranged from a recognition phase, to an approach phase, to a charge, and finally to a sustained chase. Of 65 wolf/prey encounters that we observed from an aircraft, wolves closely watched the prey in 29 cases, and in 18 incidences wolves approached but did not attack. Attacks were recorded in 17 cases, three of which resulted

in kills. On 55% of the wolf charges (12 out of 22 occasions) bison first stood their ground but then fled. In all cases where bison fled, wolves attacked. Chase distances to full-pursuits did not exceed 500 m at a time, but total distances traveled by wolves and potential prey were often long if the hunt lasted over several days.

Bison responses were partly determined by the number of previous attacks and the length of time they were exposed to wolves. The longest time that a pack remained with a herd was six days. If packs stayed with herds for three or more days, they were successful in killing a victim 100% of the time. Success of attacks tended to increase as time between kills increases. However, there was no apparent relationship between wolves increasing "active" interest in prey and elapsed time since their last kill.

Predation rates and prey selection were studied from 1978 to 1981 on 285 contact days. During this period, one pack killed 40 bison and two moose, averaging one animal every 6.8 days. The success rate of wolves preying on bulls (69%) was less than that of wolves preying on mixed herds (79%). Generally, calves and old animals were the most vulnerable component of the bison population. Of all calf and yearling kills, 41% occurred in forest cover. Carcass utilization was high in all years. Calves were consumed within one day of being killed. Carcasses of adult bison were generally abandoned before being totally consumed, but in all cases carcasses were completely utilized within one month. One pack spent an average of 2.4 days at each bison kill. Calculated food intake by wolves varied from a high of 6.4 kg per wolf per day to a low of 2.5 kg per wolf per day. Average utilization per wolf was 4.3 kg of food per day.

Wolf and bison numbers remained stable throughout the duration of the study. Wolf predation, has an impact on bison population dynamics, especially in reducing calf recruitment.

The overall impact of wolf predation increases as bison numbers decline. A combination of low calf production and wolf predation is considered to be important in bison declines. The role of diseases in bison is largely unknown and could be important in controlling reproduction in bison.

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A. Kennedy and D. Meleshko carried out laboratory analysis of wolf and bison specimens, and F. Anderka supplied the radio collars. M. Kingsley assisted with the statistical data analysis, and S. Popowich drafted the figures in the report.

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INTRODUCTION

"One of the worst, most persistent enemies the buffalo had to contend with was the wolves, which followed the herds in great packs, destroying many calves and the aged and feeble members that were usually relegated to the rear and outskirts of the herd."

From: Garretson (1938), The American Bison.

Bison (Bison bison) in Wood Buffalo National Park are part of the last remaining population of free-ranging bison to survive in co-existence with wolves (Canis lupus) as their major predator in a relatively undisturbed predator-prey system. The two species are known to have existed in this area since the earliest days of exploration (Mitchell 1976), although most likely they both occurred here prehistorically as well (Guthrie 1970).

Wolves in northern Canada and Alaska continue to retain much of their original habitat in a sparsely populated frontier, although conflicts between man and wolves over ungulate resources have occurred wherever wolves compete with humans for food. During the 1950s, in response to decreasing caribou (Rangifer tarandus) numbers, large-scale wolf control programs were conducted throughout most of northern Canada, including Wood Buffalo National Park and the adjacent Northwest Territories (Fuller 1953, 1954, 1955, 1956a; Fuller and Novakowski 1955; Kelsal 1968). More recently a dramatic decline in bison numbers in the Slave River lowlands north of the park (Van Camp 1980) inflamed local opinion that wolf predation was the

major reason for the bison decline, and resulted in the initiation of wolf-bison studies and ultimately a wolf control program.

The high public profile of the largest free-roaming bison population in the world, and its low growth rate (Fuller 1966) since the controversial introduction of about 6500 plains bison in the late 1920s, resulted in political pressure to initiate a predator-prey studies. These studies were similar to those conducted in the Northwest Territories (Van Camp 1980) where bison had declined precipitously.

Although the relationship between wolves and many prey species has received widespread study in recent years, aside from wolf control (Fuller and Novakowski 1955) and information incidental to bison studies (Fuller 1966), the interactions of wolves and bison have not been extensively investigated. This study originated as one of the sub-objectives of an ongoing Bison Research Program in the park, in order to assess the significance of wolf predation on the bison population. Fieldwork was conducted between July 1977 and April 1981, but was most intensive from February 1978 to April 1981.

The working hypothesis of this study was that wolf predation was an important factor influencing bison numbers in the park. Fuller (1966) thought that possibly wolves did not prey significantly on any but surplus and handicapped bison (compensatory mortality - Errington 1946). Short term impacts of predation may depress numbers, however, the long term effects are impossible to evaluate.

The specific objectives of this study were:

1. Determine the wolf population size, distribution and movements in the primary bison ranges of the park.

2. In collaboration with the park Warden Service, determine year-to-year changes in total bison numbers, seasonal distribution, and calf production and survival.
3. Determine prey selection and predation rates by wolves in winter.
4. Determine seasonal food habits of wolves, particularly as they related to alternate prey species, and prey selection at den and rendezvous sites.
5. Describe wolf hunting techniques and mechanisms of bison anti-predator behaviour.
6. Document snow cover conditions and winter severity in relation to bison vulnerability.
7. Examine the concept of wolf pack territoriality as it applies to the wolf-bison system.

From the onset of the study, however, it was apparent that it would be extremely difficult to extricate predation mortality from a variety of other mortality factors, such as disease and winter severity. Reduced funding and manpower in the second and subsequent years of the study resulted in data collection within a decreased study area (see below). This report incorporates earlier preliminary results reported in Oosenbrug et al. (1980a, 1980b, 1981) and Carbyn et al. (1981).

STUDY AREA

The relationship between wolves and bison was studied in Wood Buffalo National Park, a huge wilderness preserve that straddles the eastern part of the border between the Northwest Territories and the province of Alberta. The park was established in 1922, and contains an area of 44 800 km^2. The greatest length (north/south) of the park is nearly 290 km and its width varies from about 166 km in the north to 128 km in the south.

Wood Buffalo National Park lies within the Mackenzie lowlands, a northern extension of the Great Central Plains. As such the park has a gradual slope from south to north on which is superimposed an incline from west to east in four distinct steps. These four elevational units were described by Raup (1933) and Soper (1939) and include the Caribou and Birch mountains, Alberta Plateau, Salt Plains, and Peace-Athabasca-Slave River lowlands.

The climate of Wood Buffalo National Park is characterized by long, cold winters, short, cool summers, and low precipitation, nearly half of which falls as snow. Average mean monthly temperature in nearby Fort Smith ranges from -26.6°C in January to 13.8°C in July (Atmospheric Environment Service 1971). Average annual precipitation in the area is about 33 cm while normal annual snowfall is approximately 130 cm (Day 1972). Snow cover is usually continuous from early November to mid-April. The prevailing weather comes primarily from the northwest out of the Mackenzie River basin.

Throughout the year, monthly mean temperatures in the southern portion of the park (Fort Chipewyan) are generally several degrees warmer

than in the northern area (Fort Smith). Frost-free periods vary greatly between the two areas, ranging from about 58 days in Fort Smith to 102 days in Fort Chipewyan.

The park was entirely over ridden by an ice sheet during the last glaciation of the Pleistocene, which advanced from the retreated northeast approximately 9000 years B.P. As a result, post-glacial lakes covered all of the Alberta Plateau and Salt Plains (Cameron 1922). Soils of the region were derived from glacial outwash, post-glacial lake bottoms, or subsequent deposition by the major rivers in the lowlands. According to Rowe (1972) Wood Buffalo National Park lies in the upper Mackenzie section of the Boreal Forest Region. White spruce (Picea glauca), trembling aspen (Populus tremuloides) and jack pine (Pinus banksiana) form the main forest cover in the northern and upland portions of the park. These forests separate vast open meadows supporting sedge and grass communities. The meadow habitat is interspersed with stands of shrub willow (Salix spp.) and is particularly extensive in the Peace-Athabasca delta and Slave River lowlands where awned sedge (Carex atherodes) and reed grass (Calamagrostis canadensis) dominate the ground cover (Cordes and Pearce 1977). The Salt Plains is a flat, poorly drained region of large saline meadows interspersed with islands of spruce, willow and aspen. The meadows are colonized by sedges and variety of halophytic plants including glasswort (Salicornia europaea), black saltwort (Glaux maritima) and arrow grass (Triglochin maritimum).

Several communities exist in or near the park, including Fort Smith (population 2500) on the Slave River to the northeast, Fort Chipewyan (population 1100) on Lake Athabasca to the southeast, and a native

settlement at Peace Point (population approximately 30) on the Peace River within the park. Road access to Fort Smith was nonexistent until 1966, but at present unimproved roads link Fort Smith to Hay River and Peace Point year-round, and in winter a road extends from Fort Chipewyan north to Fort Smith. Visitation to the park has increased since 1966, although access to large portions of the park is difficult and the park today remains essentially an untravelled wilderness area.

Under the Wood Buffalo National Park Game Regulations a limited number of local residents (355 in 1980-81; D. Anions, pers. comm.) trap and hunt in the park as holders of General Hunting Permits. These permits are not available to the general public, but are a privilege granted to certain local hunters and trappers based on ancestral hunting rights within the park boundaries. Under the Game Regulations, wolves are classified as furbearing animals and may be shot and trapped by holders of General Hunting Permits within their defined trapping areas (see p. 77). Other fur-bearers may also be trapped, and moose (Alces alces) may be taken for subsistence purposes. Within the park boundaries, bison are completely protected, although some illegal hunting of bison is known to occur. Bison outside the park, however, are subject to hunting by both holders of Alberta and Northwest Territories General Hunting Licenses. The number shot when bison travel out of the park varies.

The selection of the study area in 1977-78 was based on: (1) The delineation of primary bison ranges (Fig. 1) as determined by aerial surveys conducted by the Warden Service in the park; (2) The location of areas of historical wolf abundance in the park; and (3) An objective to obtain comparative information on wolf pack dynamics and prey selection of:

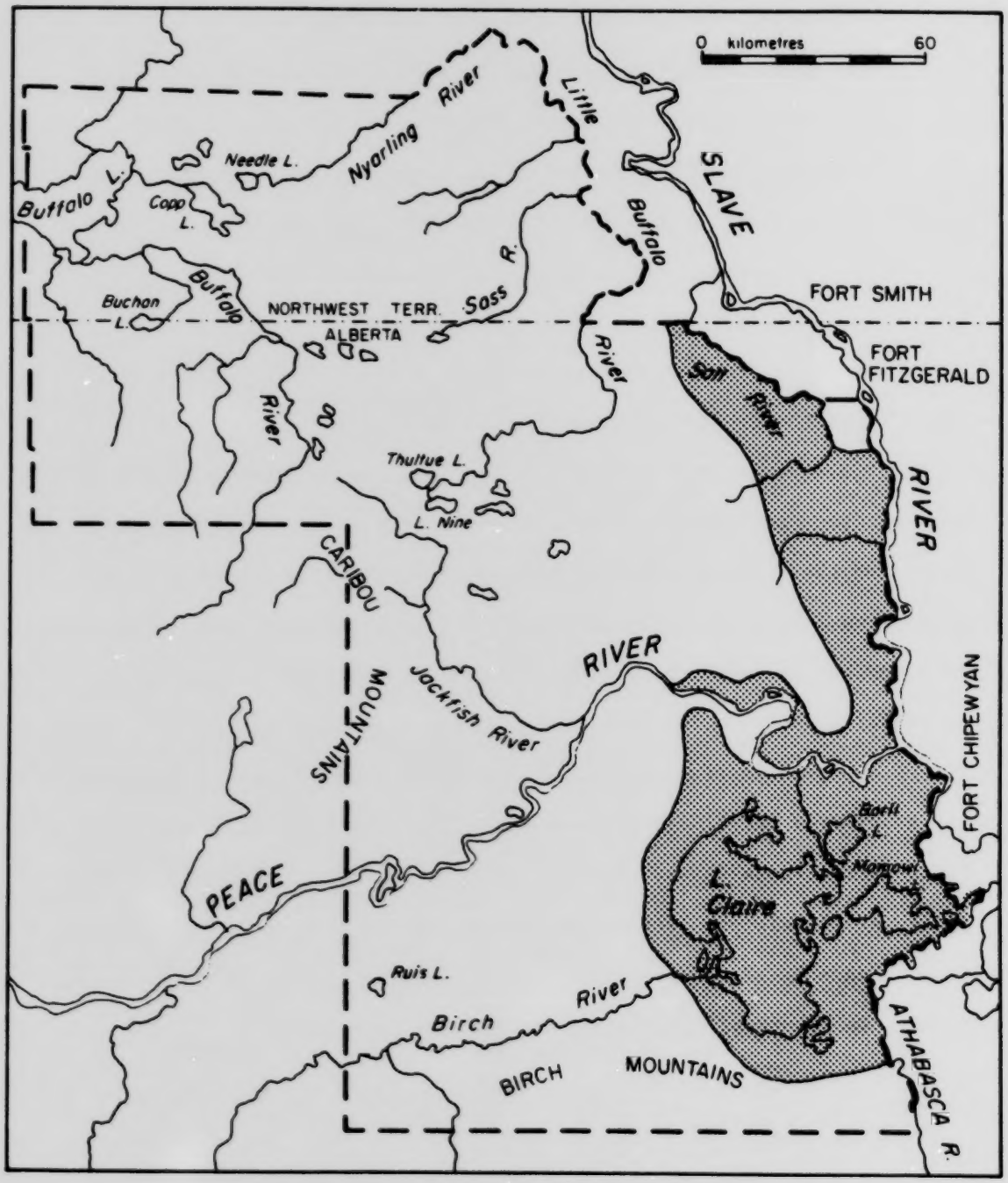


Figure 1. Primary bison ranges in Wood Buffalo National Park north and south of the Peace River (from Park Warden Service files).

a) undisturbed and exploited wolf subpopulations,

b) wolves occupying all-year versus winter bison ranges, and

c) wolves occupying primary versus secondary bison ranges.

Primary ranges are defined as areas where bison concentrations in winter are predictable and where numbers reflect consistant heavy use of the ranges. Secondary ranges cover the areas where densities are much lower, and where herds are not consistantly present.

Initially two geographically distinct areas, both primary bison range, were chosen for the study area. These were the large meadows north of the Peace River (Hay Camp and Darough Creek meadows, Raup Lake and Murdock Creek meadows), and those south of the Peace River (Peace-Athabasca delta and Lake Claire region). Additional Parks Canada funds extended the study area into adjacent secondary bison range, including the Conibear Lake area and the northwest portion of the Salt Plains which straddles the northeast boundary of the park and is subject to persistent wolf trapping.

As a result of logistical problems and reduced funding, the size of the study area in 1978-79 was reduced to the primary bison ranges north and south of the Peace River. Further logistical problems reduced the study areas for the winters 1979-80 and 1980-81 to the primary bison ranges north of the Peace River. During 1980, summer observational work was continued at Lake One south of the Peace River (Carbyn et al. 1981).

HISTORICAL REVIEW

The early history, biology and management of bison in Wood Buffalo National Park have been documented in detail by Raup (1933), Soper (1941), Fuller (1966) Mitchell (1976) and Carbyn and Anions (in prep.). Historically the wood bison Bison bison athabascae ranged throughout much of western Canada, but during the 1800s their numbers declined considerably. Raup (1933) attributed the decline primarily to hunting pressure from the fur trade and increased exploration, although he recognized local reports of large bison die-offs during severe winters. Fuller (1966) argued that the scarcity of wood bison during the 1800s was not due to human interference since Europeans in the area were few and wood bison throughout this entire time period had never been abundant. In either case, by 1890 not more than an estimated 500 bison remained in an area now covered by the northern two-thirds of Wood Buffalo National Park, and in 1893 legislation for the protection of these remnant herds was enacted by the Canadian parliament. In 1922 Wood Buffalo Park, encompassing an area of about 27 200 km^2 north of the Peace River, was created by Order in Council to protect the range of the wood bison, which were estimated to number 1500 at that time (Graham 1923).

The historical association of wolves and bison in the area of Wood Buffalo National Park was first documented at the turn of the century by Seton (1886, 1911) amidst numerous allegations by local residents that wolves were responsible for the declining bison numbers. Soper (1941, 1942) believed that wolf numbers in the park during the 1920s were considerably less than in previous times. Although wolves ranged practically throughout the park, they were considered to be more numerous

in the western section where they preyed primarily on moose (Soper 1941). An estimated 170 wolves were thought to occur in that portion of the park north of the Peace River.

By the early 1930s there seemed to have been a marked increase in wolves on the bison ranges of the park. Soper (1942) speculated that this influx was derived from increased wolf numbers on the Tazin Highlands northeast of the park. This influx was in response to a massive movement of barren-ground caribou (Rangifer tarandus) into the area during the winter of 1924-25. According to Soper, these wolves apparently spread westward into the park as the caribou retreated north in late winter. Although Soper made no mention of the coincident introduction of plains bison during the years of the observed increase in the wolf population, it is conceivable that these bison, in their weakened condition (Oldham 1947, Stevens 1954) and lacking efficient anti-predator mechanisms, provided a substantial food supply for resident wolves, and provided an impetus for the expansion of the wolf population.

According to Soper (1945) wolf numbers increased even more dramatically from 1932 to 1945, as part of what he perceived to be a circumboreal phenomenon from Alaska to Ontario. He advocated a program of wolf control, based on his own observations and those of local trappers that wolves had become extremely plentiful. He conjectured that they were killing too many bison, moose and deer (Odocoileus hemionus), especially since these ungulates provided a major source of meat for local natives. Both Soper (1945) and Mair (1954) referred to similar increases of wolf populations in Alaska (Murie 1944) and central British Columbia and surmised that wolf population fluctuations were cyclical. Murie and Mair

concluded that these fluctuations were most likely mediated through disease such as mange, rabies, or distemper. It appeared that by the early 1950s the wolf population in the park had passed a peak, and may have already been somewhat depressed by an outbreak of rabies (Fuller 1954; Ballantyne 1956), although no cases of rabid wolves were documented.

No systematic records of wolf-control programs in the park exist prior to 1949, although poisoning with strychnine started as early as the late 1930s (Br. Surreault, pers. comm.; in Mitchell 1976, Carbyn and Anions in prep.). Poisoning programs occurred every winter from 1951 to 1960 in connection with concurrent bison studies (Fuller and Novakowski 1955), in response to the threat of rabies (Fuller 1953), and as part of a control program to protect the dwindling caribou herds to the north (Fuller 1955). Accurate figures on the wolf kill during this period are not available, but a reported 227 wolves were taken by Canadian Wildlife Service and park personnel in the years 1951-52, 1952-53, 1953-54, 1957-58 and 1959-60, during which time the wolf population in the park apparently remained stable.

Wolves were again considered to be increasing by the late 1960s, as reflected by the concern of local trappers in the western portion of the park (Cooper, Colisimo 1967 - memorandum in Parks Canada files). It appears that wolves became more abundant in the park and vicinity during the late 1960s and early 1970s. South of the park, in Alberta, wolf numbers apparently increased rapidly during this time (Stelfox 1969) and seemed to have peaked in the early 1970s. Availability of numerous bison carcasses resulting from bison hunting programs north of the park (Slave River Lowlands) as well as slaughters, roundups, and vaccination programs

within the park may have contributed to increases in wolf numbers. In 1972, 326 bison were known to have died during the roundup procedures at Sweetgrass (Millette and Sturko 1977). Since the availability of such an increased food source was short in duration, it was unlikely that marked numerical responses resulted.

Records obtained from systematic bison surveys from 1972 to the onset of this study in 1977, indicated that wolf numbers on the primary bison ranges in the park were high prior to 1974 (Carbyn and Anions in prep.) but have continued to decrease to the present time. The reasons for the recent decline are not known, but may be a combination of disease, notably mange, increased hunting and trapping pressure in the Peace-Athabasca delta region during the mid-1970s, and a decreasing bison prey base.

METHODS

Collection of field data in this study was carried out year-round with a concentration on two seasonal time periods: winter (November-March), and summer (May-August). Winter field studies consisted of: (1) aerial capture and tracking, and ground tracking of wolves; (2) aerial surveys of bison; (3) collection of wolf scats and winter weather data. Summer field studies included: (1) aerial tracking of wolves; (2) ground observations of bison and wolves; and (3) collection of wolf scats.

Wolves were captured for radiotelemetry with a Cap-Chur gun and dart (Palmer Chemical and Equipment Co.) fired from a helicopter. Methods for aerial capture were similar to those described for coyotes (Baer et al. 1978), and for wolves (Van Camp 1977 and Stephenson 1978). Packs were initially spotted from fixed-wing aircraft, and selected wolves were darted from either an Alouette II, Bell Jet Ranger 206B, or Bell J-42 helicopter. Wolves were immobilized with intramuscular injections of 100 mg of phencyclidine hydrochloride (Sernylan; Parke-Davis Co.) and 50-100 mg of promazine hydrochloride (Sparine; Wyeth Laboratories), or 100 mg of xylazine (Rompun; Chemagro Inc.). In 1978-79 ketamine hydrochloride (Ketaset; BTI Products Inc.) was used as a possible replacement for Sernylan, but mixtures of 150-450 mg of Ketaset with 75-150 mg of Rompun were not potent enough to immobilize target animals.

Captured wolves were examined, weighed and ear tagged. Body measurements and canine teeth length were taken. General physical and nutritional condition was noted, and reproductive status was determined by examination of vulvae or testes. Wolves less than 21 months of age were

distinguished from adults by weight, tooth wear, and length of permanent canines (Van Ballenberghe and Mech 1975).

Canadian Wildlife Service staff in Ottawa constructed radio collars of machine belting and acrylic which were placed around the neck of each wolf. Twenty-one wolves captured in 1977-78 were fitted with collars containing 150-151 MHz transmitters. Radio interference from a local Alberta Government Telephone transmitter hampered tracking in 1978. To counteract this problem, 21 collars with frequencies of 171-172 MHz were applied in the following two years.

Instrumented wolves were located with a Bellanca Scout or Cessna 185 aircraft equipped with two, 4-element Yagi directional antennae, one mounted on each wing strut. Signals were picked up by means of a crystal-controlled AVM model LN 12 manual receiver. Under optimum conditions signal range of the transmitters at 2000 m asl was approximately 60 km. The aircraft was directed toward the signal source by alternately switching reception from one antenna to the other until the signal was of maximum and equal strength at both antennae. When located, wolves were circled repeatedly at 500 m until seen and their activity determined. When wolves were obscured by heavy cover, only a brief effort was made to sight them. Locations of instrumented wolves were plotted on 1:54,000 scale aerial photographs and later transferred onto topographical base maps (scale 1:250,000).

Wolves captured in February and March 1978 were located at 2-4 day intervals during late winter, and more irregularly from May to September 1978. Intensive radio tracking flights at 1-3 day intervals occurred from January to early April 1979, in December 1979, mid-January to early April

1980 and from mid-January to mid-April 1981. A total of 330 flights (746 hours), was flown during the study, resulting in 943 locations of instrumented wolves. Wolves were observed 543 times, and the rate of observation of instrumented wolves ranged from 14% in May-September 1978 to 90% in November-April 1980-81. Wolves generally are territorial (Van Ballenberghe et al. 1975, Fritts and Mech 1981, Carbyn 1980). It appears that some wolf populations with a mobile prey base such as caribou do not occupy exclusive, year-round territories (Stephenson and James 1982). This aspect was examined in this study and rather than assuming territoriality a wider concept of home range was employed.

Home range size for instrumented wolves was determined in several ways. The polygon-perimeter method of Mohr (1947) was used to compare size and shape of home range with results of other published wolf studies. Adequate measurement of the home range sizes was determined by plotting the cumulative number of locations in relation to the area occupied by means of a modified "species area" curve (Odum and Kuenzler 1955; Tester and Siniff 1965). Home range sizes were considered adequately defined when the curve of the area reached an asymptote. Multiple asymptotes represented expansion, or seasonal or year-to-year shifts of home ranges (Carbyn 1980).

A second method was based on the premise that the entire area within the polygon was probably not used by the wolves and this did not give a realistic estimate of home range size. In this case, perimeter location points were connected only if they were less than one-fourth the distance between the most distant location points (Harvey and Barbour 1965). All points farther apart were eliminated from the home range calculation.

Home range size was also determined by calculating the geometric mean centre of activity (Hayne 1949) and expressing home range sizes in terms of the mean activity radius (Dice and Clark 1953); Tester and Siniff (1965). The latter expression was used to describe the core area of the home range. Finally, home range size was estimated by the atypical-habitat elimination method (Ables 1969), whereby areas distinguishable by physical features from the usual range of instrumented wolves, and seldom visited by the wolves, were excluded from calculation of area.

Frequency-distribution graphs of location distances from the geometric mean activity centre were used to assess territoriality, dispersal and home range boundaries. Area utilization within the home range was determined by dividing the area into arbitrary square units of 6.25 km^2, similar to methods described by Tester and Siniff (1965) and Ables (1969), and plotting the frequency distribution of the number of locations in each of these squares.

Wolf numbers, densities and numerical trends from year to year in the primary bison ranges were determined from aerial searches for wolves, observations of wolves in aerial bison surveys, and radiotelemetry information. Extrapolation of wolf numbers from instrumented packs on part of the primary bison ranges to the entire area assumed a consistent density throughout, and included an additional 10% for lone wolves. This technique was similarly used by Pimlott et al. (1969), Mech (1973, 1977b), Fuller and Keith (1980) and Carbyn (1980).

Summer homesites of wolves were located by radiotelemetry, observations during aerial bison surveys, and ground investigation. Areas of habitual summer use were described by expressing the number of locations of

instrumented wolves in these areas as a proportion of the total number of locations during the summer. Locations were mapped, and when accessible were visited on foot and examined for activity and collection of scats. Attempts were made to record the number of pups and adults present at known homesites by observation or induced howling (Joslin 1967). Howling was also used to identify homesite areas adjacent to the park road system and hiking trails.

The reproductive condition of wolves submitted to the warden service by local trappers was determined by histological examination of the ovaries and uteri of adult females. All wolf carcasses were examined for nutritional condition, external parasites, and physical infirmities. The incidence of mange (Sarcoptes scabiei) was estimated from aerial observation of wolves and examination of captured wolves and carcasses. The impact of hunting and trapping on the wolf population was estimated by examination of park, Northwest Territories and Alberta fur harvest records, as well as personal communication with local trappers.

Parameters of bison population dynamics have been determined by the park Warden Service since 1972, and survey methods were reviewed earlier (Stelfox 1975; Carbyn and Anions 1984). During the study, surveys consisted primarily of an annual total count in February, distribution and migration surveys in spring and fall, calf production and survival surveys in June, August, November and February, and anthrax surveillance flights in summer. Changing bison management objectives have resulted in fewer surveys overall and increased multiple-purpose surveys since 1979 (Carbyn and Anions in prep.).

Results of annual midwinter total counts from 1977-78 to 1980-81 were used to describe an overall year-to-year pattern of bison distribution. Bison locations (singles and herds combined) were plotted within a systematic 300-point grid of the Raup Lake, Hay Camp, Darough Creek, and Murdock Creek meadows (Fig. 2), and distances from each point to the nearest bison were measured, ranked, compiled into 10 equidistant groups, and graphed as to determine uniformity and dispersal in distribution (see Fig. 35).

Additional bison surveys were conducted in conjunction with wolf-tracking flights north of the Peace River during winters 1979-80 and 1980-81. These surveys were to determine day-to-day movements of herds and juvenile survival. Bison numbers and distribution for early, mid, and late winter were calculated for the home range of the Hornaday River pack. Patterns of distribution for the Hornaday River pack were related to the relative abundance of bison within the pack's winter home range, as well as to the midwinter distribution of bison determined from the 300-point grid described above.

The Hornaday River pack was radio tracked daily by aircraft from 19 February to 6 April 1979 to determine its winter movements, hunting behaviour, prey selection and predation rate. Concurrent ground tracking by snow machine or skis was used to examine wolf-killed bison, scavenged carcasses, and to verify travel routes and behaviour of the pack. The same pack was intensively tracked from 3-31 December 1979, 18 January to 7 April 1980, 9-31 December and 21 January to 14 April 1981 to compare early winter versus late winter movements and predation patterns. All pack locations,

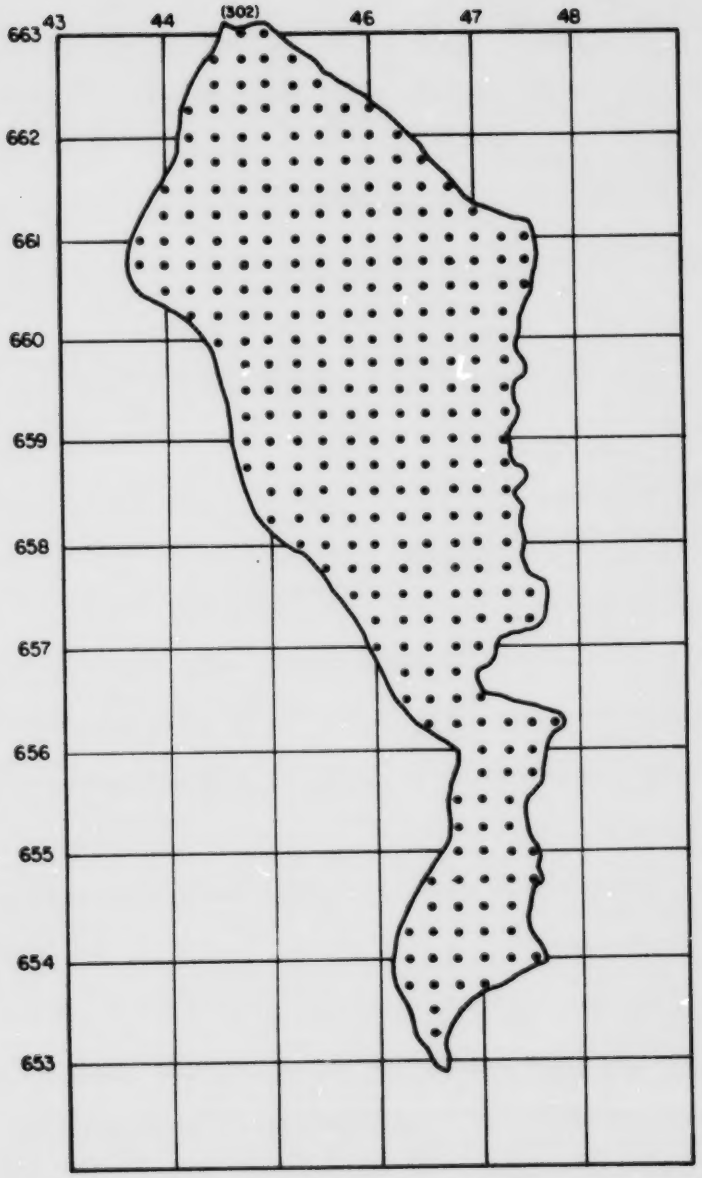


Figure 2. Systematic 300-point grid of the Raup Lake, Hay Camp, Darough Creek, and Murdock Creek meadows, used to describe bison and associated wolf distribution in Wood Buffalo National Park, winters 1977-78 to 1980-81.

kill sites, travel routes and chase sequences were marked and measured on 1:54,000 aerial photographs.

Confirmed or suspected wolf kills were examined whenever possible. Prior to 1978 information on wolf kills was collected exclusively by the Warden Service, but from 1978 to 1981 most carcasses were examined by the research team. Notes were made on habitat, snow conditions, track evidence of a chase and/or struggle, approximate age, sex and condition (if possible) of prey, obvious physical infirmities, and proportion consumed. Consumption of prey was quantified by using a scale from 1 to 4 (Pimlott et al. 1969). Hornaday River pack, kills were not examined until after the wolves had voluntarily abandoned the kill site. Kills not completely consumed were periodically reexamined to determine the frequency of revisits by wolves.

Where possible, lower jaws and femurs were collected from each carcass. Incisors were sectioned (Sergeant and Pimlott 1959), decalcified, and cemental layers read (Armstrong 1965). Bone marrow was removed from the femur and analysed for fat content (Verme and Holland 1973). Portions of the skeletal remains were collected, examined for anomalies, and deformities were analysed.

Although tenuous, the estimated age structure of the bison population in the park was determined from roundup figures at Hay Camp (Novakowski and Choquette 1963) and Sweetgrass (Novakowski and Choquette 1964), the 1971 field slaughter (Currier 1971), and early winter calf surveys from 1978 to 1980. The age structure of wolf-killed bison was compared to the estimated age structure of the population, and differences were evaluated by means of Chi-square analysis. Obviously such a

comparison cannot be considered accurate, however, it is the best that can be done in the absence of time specific life tables. The values of adult bison mortality were set arbitrarily to carry out calculations on a model. Another method would be to assume that all total counts and recruitment figures are accurate. Thereby mortality figures could be derived from actual survey data.

Wolf scats were collected year-round at kill sites and carcasses, on trails and on roadways. In summer, collections were also made at dens and rendezvous sites. Scat size overlap could occur with coyotes (Canis latrans), but these were uncommon in the study area. Scats with a diameter less than 25 mm were not collected unless they were suspected to be wolf-pup scats at a den or rendezvous site.

Date of scat deposition was recorded as accurately as possible. Field personnel were instructed to collect only scats that had obviously been recently deposited, and these were assigned monthly age categories. Precise dating occurred for certain roadways and trails searched at 2-6 week intervals in summer 1979 and 1980 (see Appendices). Scats collected at summer homesites of instrumented and non-collared packs were dated according to period of known occupany. Scats for which accurate deposition dates were not available were included in one of six categories, namely early summer (May-June), midsummer (July-August), late summer (September-October), early winter (November-December), midwinter (January-February), and late winter (March-April).

Identification of hair in the scat samples was determined by gross examination of hairs and comparison to known material, as well as microscopic examination of hair medullae and scale pattern (Adorjan and

Kolenosky 1969; Kennedy and Carbyn 1981). Scat contents were grouped into 11 categories based on identified food items. In some cases (9.1% of total sample), multiple food items occurred in the same scat. For that reason food items were expressed as a percentage occurrence of total food items recovered from the scat samples, although the volumetric proportion of each food item in each scat (Lockie 1959) was not determined. Spatial and temporal differences in occurrences of food items were tested for significance by Chi-square analysis (Fritts and Mech 1981).

Relative biomass and numbers of different species in the diet were calculated by means of a linear regression developed by Floyd et al. (1978) to describe the relationship between number of collectible scats and weight of the prey consumed. Figures for biomass and numbers for bison in both summer and winter were by necessity derived from the winter sex and age ratio of bison killed by instrumented wolf packs, since it was impossible to distinguish bison calf hair from that of adults at certain times of the year.

Behavioural studies of bison, wolves and wolf-bison interaction were conducted during the summers of 1978, 1979 and 1980 at Lake One, south of the Peace River. This area is an important summering range for bison in the Peace-Athabasca delta and contained a resident pack of wolves from at least 1977 to 1981. Observations were carried out primarily from an elevated 3.5 m tower, and were supplemented by ground observations. Observation periods varied from 10 to 30 days each month from May to October, but were most consistent in 1980 (Carbyn et al. in prep.). Total observation days were 97, 79 and 110 days in 1978, 1979 and 1980, respectively.

Bison numbers at Lake One were estimated by identifying herds and individuals in view from the tower, as well as those observed during hikes in the adjacent meadows. Bison were tallied daily and totalled monthly to document changing numbers throughout the summer. Classified counts were obtained in all cases where herds could be identified into male-female-calf (young-of-the-year) -yearling (young-of-last-year) components, and the results cumulated for estimates of sex ratios and age structure.

Records of wolf sightings were made to document numbers of adults and pups, behaviour at dens and rendezvous sites, hunting behaviour, and reaction to human disturbance. Spontaneous and induced howling sequences were used to supplement sightings to determine the location of homesites and movements of wolves in the area. Encounters between wolves and bison were described in detail similar to those recorded during aerial observations in winter. Particular emphasis was placed on testing the method of attack by wolves, as well as bison defense mechanisms.

Data on temperature and snow conditions were collected by Atmospheric Environment Service personnel at the Fort Smith and Fort Chipewyan airports, and at various stations in the park. Park stations were situated in open meadows, in areas commonly used by bison during the winter months. Weather information in the park was collected to assess winter severity in relation to bison welfare (Stelfox and Sturko 1977).

Measures of one or more of snow depth, density, and crust conditions in the park were obtained at 2-4 week intervals from November to April. North of the Peace River one station (Hay Camp) was sampled in 1977-78, three (Hay Camp, Darough Creek, Murdock Creek) were sampled in 1978-79 and 1979-80, and two (Hay Camp, Murdock Creek) were sampled in 1980-81. In the

Peace-Athabasca delta data were collected from three stations (Sweetgrass Station, Alfred's Lake, East Twin Lakes) in 1978-79, and one station in 1979-80 (Fig. 3).

Snow density and snow crust values were calculated for three stations north of the Peace River (Hay Camp, Darough Creek, Murdock Creek) in one or more of the three winters 1978-79 to 1980-81. Snow densities and hardness in these open meadows were probably higher than sub-canopy (forest) densities, due to compaction from wind and direct sunshine, but in light of the importance of these areas' as preferred bison habitat, these higher values were thought to most accurately describe snow conditions in terms of foraging ability and energy expenditure by bison.

At each location 10 sampling points 30 m apart along a 300 m transect were measured. At each sampling point snow depth was recorded to the nearest cm. During 1978-79 and 1979-80 snow density was calculated by weighing a 250 ml sample of snow from the centre of the snow horizon. In 1980-81 snow density values were determined by weighing a column of snow from the entire snow horizon by means of a hollow graduated aluminum cylinder (Fig. 4) and expressing the snow's weight as gm/ml volume. Snow crust values were based on a subjective scale rating from 0 to 4 (Table 1). Monthly mean temperature values from November to April were obtained at Hay Camp, Darough Creek and Murdock Creek by continuous-recording thermographs (1978-79 to 1980-81) or weekly maximum-minimum readings (1977-78).

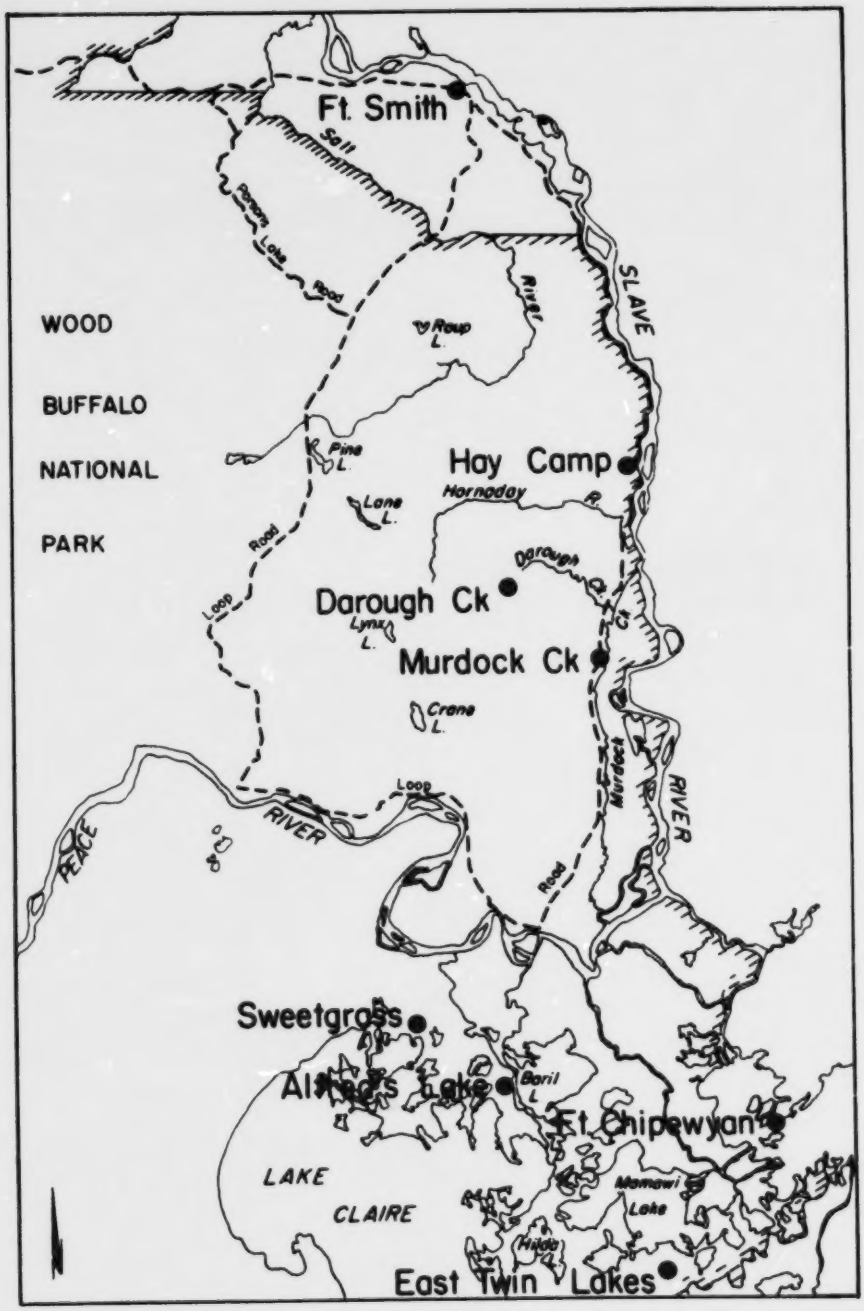


Figure 3. Location of eight sites for purposes of temperature, snow depth, snow density and snow crust measurements during winters 1978-79 to 1980-81.

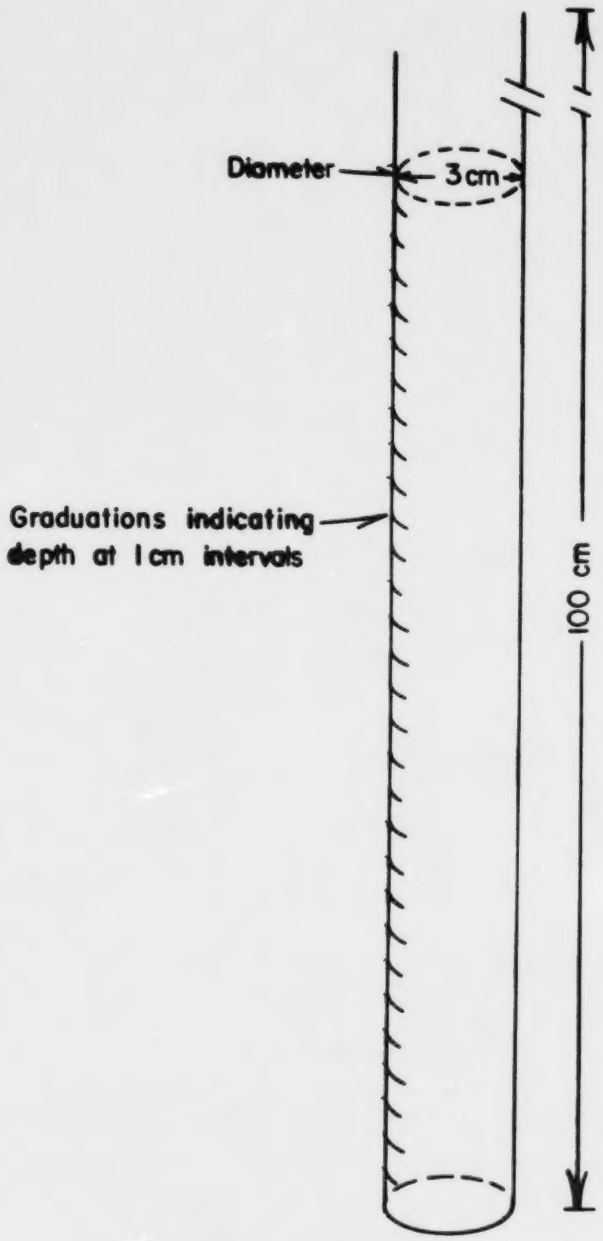


Figure 4. Hollow aluminum cylinder used for measuring snow depth and snow density during winter 1980-81 in Wood Buffalo National Park.

Table 1. Subjective rating scale used to describe surface snow-crust conditions during winters 1977-78 to 1980-81 in Wood Buffalo National Park.

Hardness	Value	Factors
None	0	No crust
Light	1	Supports mice, shrews, hares
Moderate	2	Supports foxes, lynx
Hard	3	Supports wolves
Very hard	4	Supports man

RESULTS AND DISCUSSION

A. Temperature and snow conditions

1. Measures of winter severity

A broad measure of winter severity for bison during the study was determined from comparisons of monthly mean temperatures, snowfall and snow depths collected at two stations in the vicinity of Wood Buffalo National Park (Fort Smith, Fort Chipewyan) for which long-term normals were available (Atmospheric Environment Service 1982). On this basis, (Table 2) winters were designated as mild (1979-80), and mild to moderate (1977-78, 1978-79 and 1980-81).

Temperature data collected at Fort Smith, Fort Chipewyan, and three stations within the park (Fig. 5) indicated that lowest winter monthly means occurred in December, 1977-78 and 1980-81, in January, 1979-80, and in February, 1978-79. Lowest monthly means were consistently less at all stations in the coldest winter (1978-79) and were highest in 1980-81 (Fig. 5). Although winters in Fort Smith are normally somewhat colder than in Fort Chipewyan, these differences were reversed during the winters of study except for 1978-79 (Table 2).

Snow depths for eight stations in the park were determined bimonthly for one or more winters from 1977-78 to 1980-81. These data indicated that although snow was generally deepest in March (Table 3; note Hay Camp in February 1978 and April 1981), the pattern was not consistent between localities in any one year (Fig. 6).

A comparison of snow depths at three stations (Fort Smith, Hay Camp, Fort Chipewyan) from which records were obtained for all four winters (Fig. 7), showed similar differences between stations north and south of

Table 2. Monthly measurements of temperature (°C), snowfall and snow depth (cm) at two stations in the vicinity of Wood Buffalo National Park, winters 1977-78 to 1980-81. Depths are means of measurements taken on the 15th and last day of each month (from Canadian Climate Normals 1951-1980, and Atmospheric Environment Service files, Edmonton).

Winter	Station	November			December			January			February			March			April			December to April		
		Temperature	Snowfall	Snow depth	Temperature	Snowfall	Snow depth	Temperature	Snowfall	Snow depth	Temperature	Snowfall	Snow depth	Temperature	Snowfall	Snow depth	Temperature	Snowfall	Snow depth	Mean Temperature	Total Snowfall	Mean Snow depth
1977-78	1[1]	-11.0	20.3	11.5	-26.6	21.0	29.5	-23.8	12.6	33.5	-15.5	1.0	33.0	-13.2	8.7	34.5	-2.3	14.9	13.5	-15.4	78.5	25.9
	2	-11.0	29.2	11.0	-26.3	28.1	31.5	-24.1	12.1	49.0	-16.4	0.6	49.0	-13.1	29.2	52.5	-3.3	32.7	24.5	-15.7	131.8	36.3
	Mean	-11.0	24.7	11.3	-26.5	24.6	30.5	-24.0	12.4	41.3	-16.0	0.8	41.0	-13.2	19.0	43.5	-2.8	23.8	19.0	-15.6	105.3	31.1
1978-79	1	-12.6	8.1	5.5	-23.3	23.7	25.0	-23.4	3.9	31.0	-31.9	8.1	36.5	-16.7	13.2	42.5	-6.4	18.5	20.5	-19.0	75.5	26.8
	2	-12.1	18.8	10.5	-23.7	30.8	24.5	-23.2	6.6	24.5	-30.8	18.5	32.0	-15.4	44.0	40.5	-5.0	21.8	13.5	-18.4	140.5	24.3
	Mean	-12.4	13.5	8.0	-23.5	27.3	24.8	-23.3	5.8	27.8	-31.4	13.3	34.3	-16.1	28.6	41.5	-5.7	20.2	17.0	-18.6	108.7	25.6
1979-80	1	-6.3	10.0	7.5	-15.4	21.0	23.0	-24.4	25.4	42.0	-16.7	8.7	41.0	-13.6	3.6	42.0	+5.7	0.2	3.0	-11.8	69.9	26.4
	2	-6.3	3.4	1.0	-19.0	20.9	15.0	-28.8	23.2	25.0	-22.2	16.6	31.0	-19.7	14.0	25.0	-0.9	6.0	0.0	-16.2	84.1	16.2
	Mean	-6.3	6.7	4.3	-17.2	21.0	19.0	-26.7	24.3	33.5	-19.5	12.7	36.0	-16.7	8.8	33.5	+2.4	3.1	1.5	-14.0	76.6	21.3
1980-81	1	-7.0	27.4	14.5	-19.3	23.8	27.0	-12.2	17.8	29.0	-17.6	19.01	39.0	-7.9	21.5	35.0	-4.8	21.5	21.0	-11.5	131.0	27.6
	2	-7.0	31.0	10.5	-27.0	39.0	32.0	-11.6	15.2	38.0	-16.7	20.4	39.5	-8.0	15.8	40.5	-8.7	34.5	21.0	-13.2	151.4	30.3
	Mean	-7.0	29.2	12.5	-23.2	31.1	29.5	-11.9	16.5	33.5	-17.2	19.7	39.3	-8.0	18.7	37.8	-6.8	28.0	21.0	-12.3	143.2	28.9
Normals[2]	1	-11.6	28.8	17.5	-21.6	24.9	31.0	-26.8	21.4	42.5	-21.8	18.4	49.0	-14.8	15.9	46.5	-2.2	13.5	15.0	-16.5	122.9	33.6
	2	-10.9	24.9	12.5	-20.7	27.4	29.5	-26.1	21.3	48.5	-20.7	18.2	59.5	-14.1	16.5	57.0	-1.3	23.4	9.5	-15.6	131.7	36.1
	Mean	-11.3	26.9	15.0	-21.1	26.1	30.3	-26.5	21.4	45.5	-21.3	18.3	54.3	-14.5	16.2	51.8	-1.8	18.5	12.3	-16.1	127.4	34.9

[1]Station 1 = Fort Smith, Northwest Territories; station 2 = Fort Chipewyan, Alberta.
[2]Fort Smith 1951-1980.
Fort Chipewyan 1967-1980.

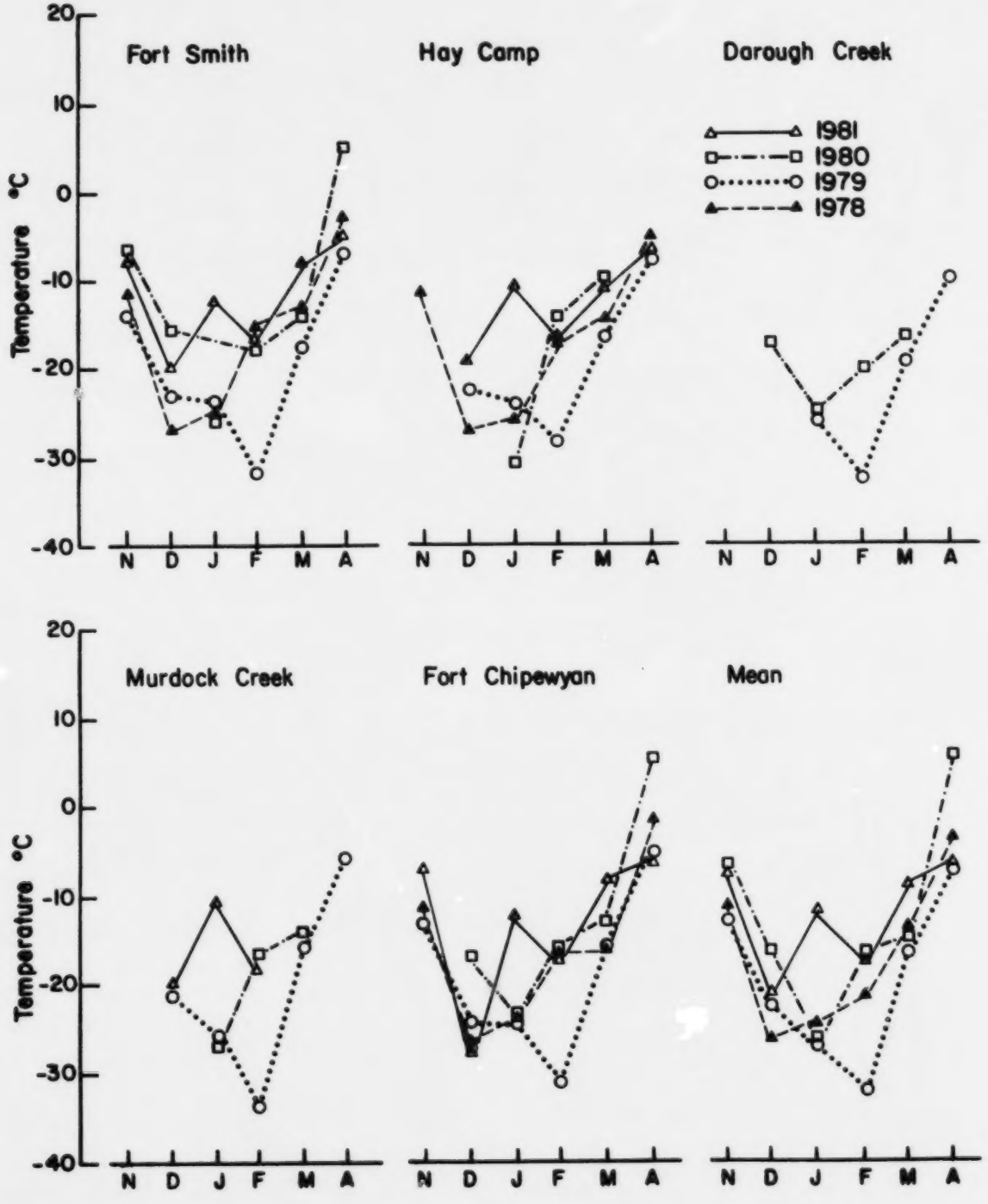


Figure 5. Comparison of monthly mean temperatures for five stations within and in the vicinity of Wood Buffalo National Park, winters 1977-78 to 1980-81.

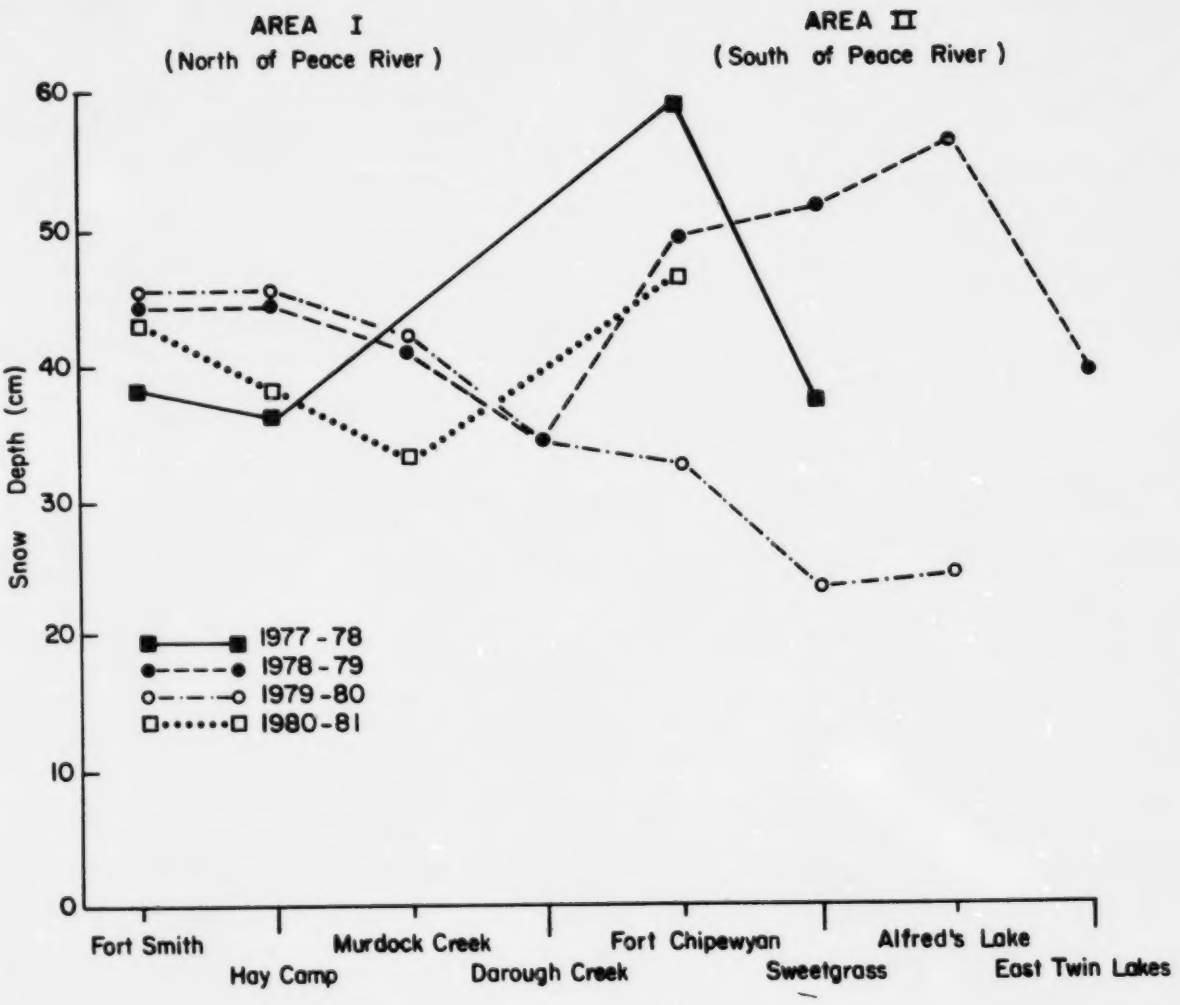


Figure 6. Comparison of maximum snow depths at eight stations within and in the vicinity of Wood Buffalo National Park, 1977-78 to 1980-81.

Table 3. Snow depth measurements on primary bison ranges of Wood Buffalo National Park, winters 1977-78 to 1980-81.

Winter	Station	Snow depth (cm)											
		Nov.		Dec.		Jan.		Feb.		Mar.		Apr.	
		15	30	15	31	15	31	15	28-9	15	31	15	30
1977-78	Fort Smith	5	18	24	35	32	35	34	32	34	35	27	0
	Hay Camp	5	15	20	25	29	36	27	28	28	29	20	0
	Fort Chipewyan	7	15	21	41	46	52	52	46	58	47	48	1
	Sweetgrass				24	28	29		31	36	37		
1978-79	Fort Smith	3	8	19	31	30	32	38	35	44	41	27	14
	Hay Camp			21	31	34	33	37		44	36		
	Darough Creek							31			34		
	Murdock Creek			20	29	30	32	34		41	33		
	Fort Chipewyan	6	15	24	25	25	24	30	34	46	35	23	4
	Alfred's Lake			38	40	40	47	48	56	55	52	41	
	Sweetgrass			22	27	30	35	36	51		41	25	
	East Twin Lakes			26	24	33	31	25	39	34	37	24	
1979-80	Fort Smith	2	13	21	25	42	42	40	42	45	39	6	0
	Hay Camp			35			44	44		45			
	Darough Creek					31				34			
	Murdock Creek			36		39		42					
	Fort Chipewyan	0	2	14	16	24	26	32	30	31	19	0	0
	Alfred's Lake			23	23	23	23	23	24	24			
	Sweetgrass			14	20	23		23	21	20			
1980-81	Fort Smith	8	21	22	32	30	28	35	43	38	32	42	0
	Hay Camp		13	23	29	32	32	31	33	29	33	38	0
	Murdock Creek		15	21	25	31	32		33				
	Fort Chipewyan	4	17	24	40	45	31	33	46	42	39	40	2
Normals[1]	Fort Smith	14	21	28	34	39	46	49	49	49	44	26	4
	Fort Chipewyan	9	16	24	35	44	53	58	61	62	52	19	0

[1]Fort Smith 1955-1980.
Fort Chipewyan 1967-1980.

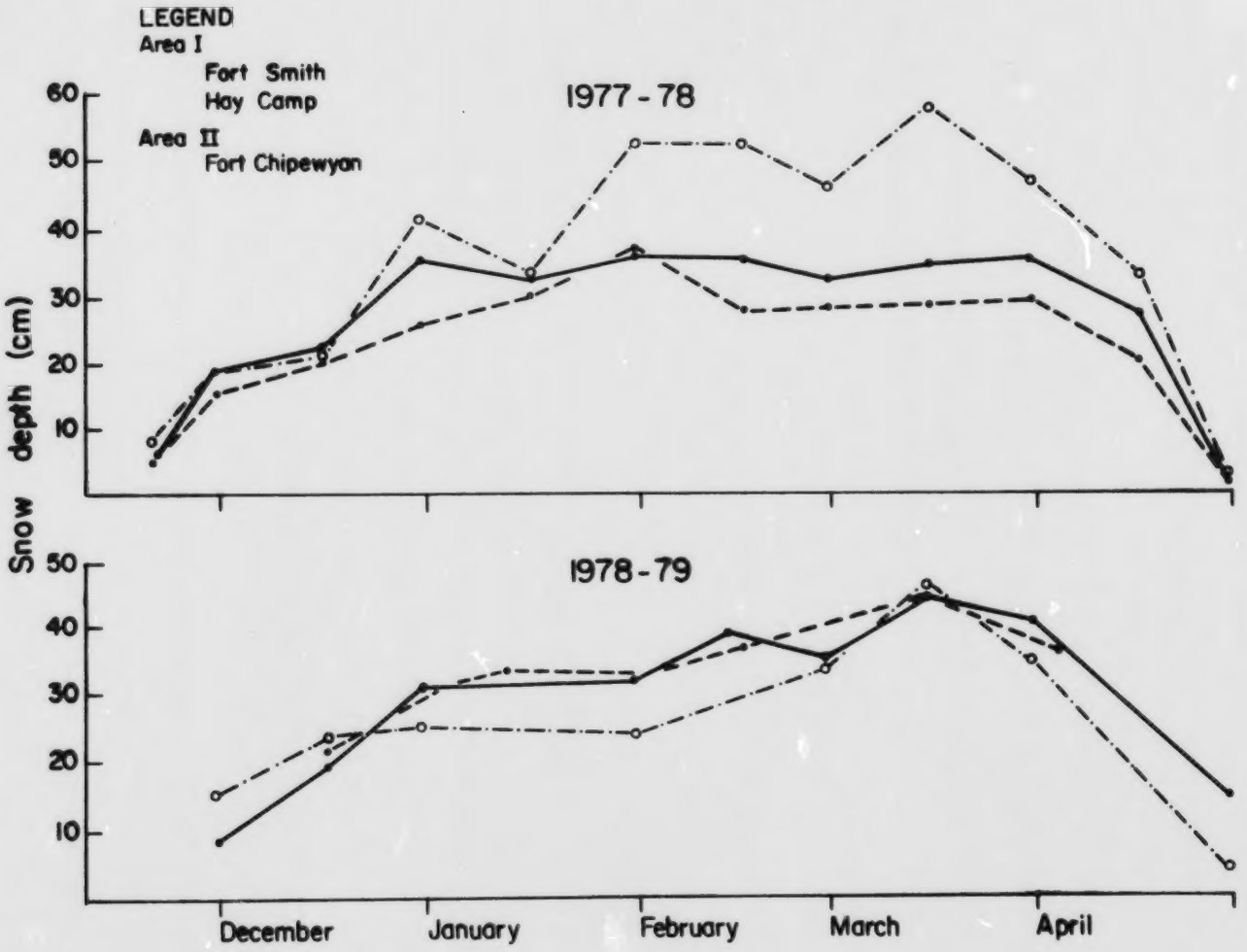


Figure 7. Comparison of snow depths on bison ranges in Area I and Area II in Wood Buffalo National Park during winters 1977-78 and 1978-79.

the Peace River from year to year. These are probably best explained by variation in local topography, yet the study area was large enough that regional weather patterns could be responsible.

An analysis of snow density values collected at three park stations north of the Peace River (Hay Camp, Darough Creek, Murdock Creek) in winters 1978-79 to 1980-81 showed that in the first two winters snow density increased as the winter progressed (Fig. 8), with temporary declines in density most likely the result of recent snowfall and lower temperatures.

Snow density in 1980-81 showed no apparent pattern of increase from early to late winter. The reasons for this are unknown, but it is possible that the different methods used that winter to calculate density may have been the cause.

Snow crust conditions were often the most difficult parameter to measure in the field, as throughout the course of the winter multiple crusts developed within the snow horizon. Crusting appeared to be primarily a process of melting and refreezing of the snowpack surface, or a result of rainfall followed by refreezing. These conditions are dependant on large temperature fluctuations which normally do not occur in the park region until late winter. However, in some years freezing rains occur sporadically in any month of the winter; this situation occurred in early February 1980-81. Crusting, as a result of compaction due to extreme wind action combined with low temperatures, occurred locally in areas of natural "snow fences", i.e. willow growth, tall grasses.

Only the upper snow crust was subjectively described as being able to support a given species of mammal (see Methods). The results tentative-

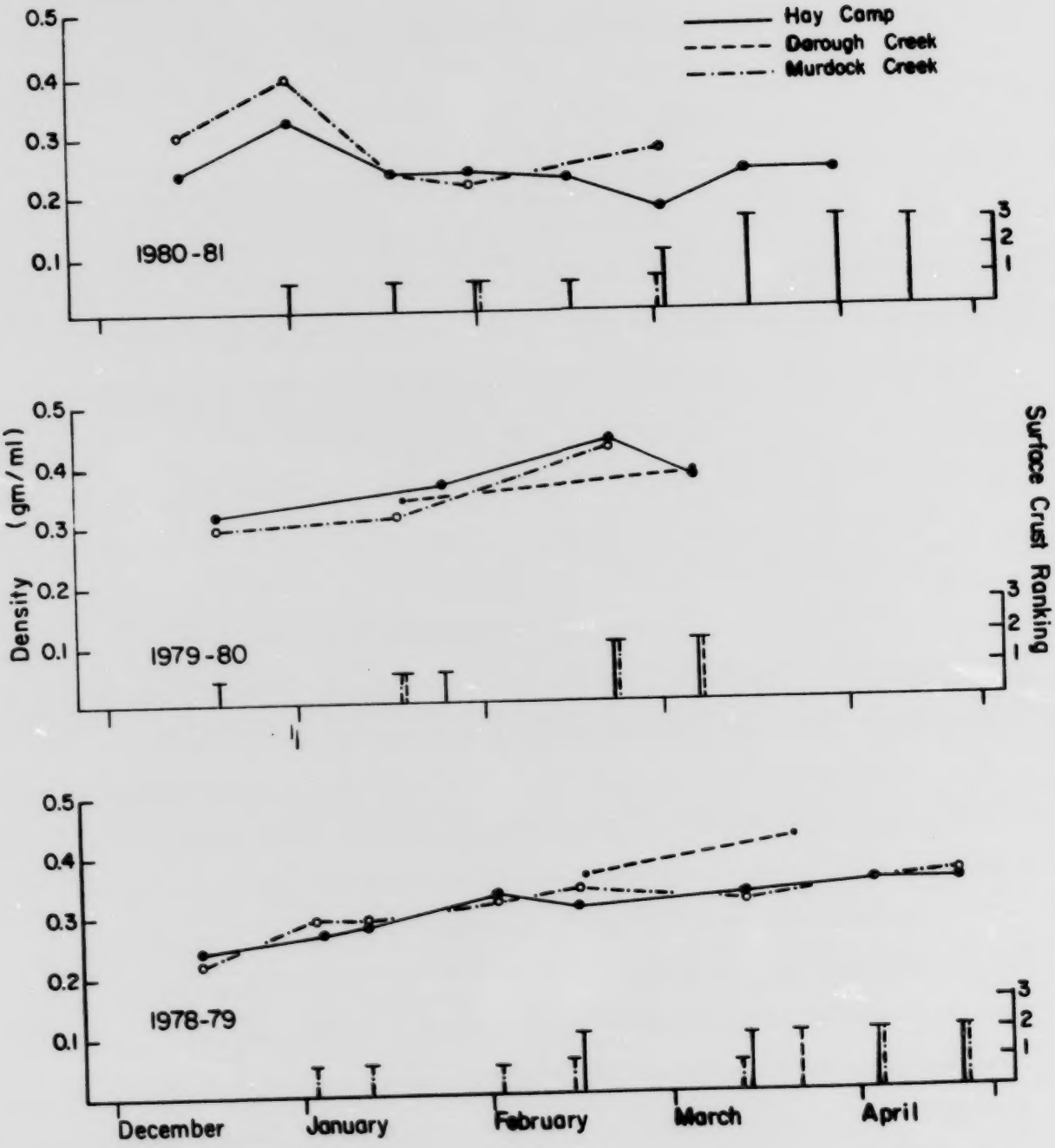


Figure 8. Comparison of snow density and crust conditions at three stations within Wood Buffalo National Park, 1978-79 to 1980-81.

ly indicate that crusting became more severe in late winter, and appeared to be consistent between stations in any given year.

2. Winter synopses

There remains an obvious need to assess current techniques of collecting snow data under field conditions, and to standardize these if meaningful interpretation is to be made of winter severity as it relates to bison welfare. However, despite the limitations of the present data, they are nevertheless useful in subjectively assessing each winter's severity. A summary of winter conditions for each year of the study follows, as these bear upon bison movement patterns, energetics and ultimately vulnerability to wolf predation.

1977-78

The winter of 1977-78 was characterized by lower than normal temperatures in December and April, but was milder than usual throughout the other months. Coldest days in December were -45.5°C at Fort Smith (6 December) and -49.9°C at Fort Chipewyan (7 December). Total snowfall was light at Fort Smith, and greater than normal at Fort Chipewyan, which received nearly half of its total snowfall during March and April.

Maximum snow depth (38 cm) at Fort Smith occurred in early January, and remained at similar depths until early April. At Fort Chipewyan negligible snowfall and above normal temperatures in late February resulted in a decrease in snow depth before snow depth increased rapidly in early March. Snow depth began to decrease in late March, and decreased rapidly after mid-April. All snow had disappeared by the end of that month.

1978-79

Temperatures during the winter of 1978-79 for most months were slightly below normal. At Fort Smith temperatures during January were somewhat higher than usual (Table 2), but this pattern was reversed from February to winter's end. The coldest day at Fort Smith was recorded on 13 February (-47.6°C). A similar pattern occurred at Fort Chipewyan, where the low dropped to -44.8°C on 2 February. Lowest temperatures were also recorded in February at Hay Camp, Darough Creek, and Murdock Creek stations.

Of particular significance were the unusually low temperatures in April, which resulted in a slower decrease than normal of snow depth on the bison ranges. Although total snowfall at Fort Smith was less than normal, consistently low temperatures resulted in a gradual accumulation of snow to a maximum depth of 44 cm on 11 March. By 30 April, 14 cm remained on the ground, and snow did not entirely disappear until mid-May. Similar patterns of accumulation and reduction of snow occurred at the six stations in the park, as well as Fort Chipewyan, although here maximum snow depth (49 cm) was somewhat less than the previous winter (59 cm), despite a similar total snowfall (Table 2).

Snow density at the three park stations north of the Peace River gradually increased from 0.24 in mid-December to 0.35 in mid-April (Fig. 8). Surface crusts were absent at Hay Camp until mid-February and did not exceed a ranking of two during the course of the winter. Crusts ranking (1) developed earlier (3 January) at Murdock Creek, but here also did not exceed (2) later in the winter (Fig. 8).

1979-80

The winter of 1979-80 was milder than normal at both Fort Smith and Fort Chipewyan, although this was more pronounced at Fort Smith (Table 2). Temperatures at Fort Smith were higher than normal during January, February and March. January was the coldest month at each station, Fort Smith recorded a low of -43.0°C on 12 January, and Fort Chipewyan -41.0°C on 11 January.

Total snowfall and snow depth were less than normal at both stations, and also less than in 1978-79 (Table 2). In contrast to the previous winter, above normal temperatures at both stations during late winter, particularly in April, combined with low precipitation, resulted in a rapid decrease in snow depth and virtual disappearance of snow by mid-April.

Snow density and snow crust information was collected from mid-December to early March. Until the third week in February snow density at Hay Camp and Murdock Creek increased from 0.31 and 0.29 to 0.43 and 0.42 respectively (Fig. 8), the upper values reflecting compaction resulting from wind action and unusually warm temperatures. Crusting was similar to 1978-79, values increasing at both stations from rankings of 0 to 2 during this time. Decreasing temperatures between 21 February and 6 March along with recent snowfalls resulted in a lower snow density of Hay Camp in early March. Snow conditions in the park were not recorded after 6 March as warm temperatures from mid-March on made road access impossible.

1980-81

Temperatures during the winter of 1980-81 were generally above normal, with exceptions in December for Fort Chipewyan and April for Fort

Smith and Fort Chipewyan (Table 2). January was unusually mild, mostly due to six days of above freezing temperatures during the third week of the month. Coldest temperatures occurred in February, with minimums of -41.3°C in Fort Smith, and -42.5°C in Fort Chipewyan, both on 11 February.

Snowfall at both stations was greater than normal, particularly in March and April, but frequent thaws throughout the winter resulted in less than normal snow depths in all months except April (Table 2). Snow density at Hay Camp increased from mid to late December, decreased by mid-January, then remained relatively constant into late March (Fig. 8). Density values at Murdock Creek also were highest in late December, and decreased by mid-January, but gradually increased during February and March.

Crusting became more severe as the winter progressed (Fig. 8), and was aggravated by freezing rain in mid-February, as well as extreme variations in temperature throughout the winter. Although snow cover in 1980-81 was not unusually persistent (Table 3), a combination of heavy crusting, high snowfall and low temperatures made April 1981 the most severe month on record during the study (Table 2).

B. Wolves

1. Capture data and fate of collars

A total of 43 wolves was captured and radio collared in Wood Buffalo National Park from February 1978 to March 1981. Three of these were caught in snares of leg-hold traps set by local trappers; the remainder were captured with tranquilizer guns fired from helicopters (Table 4).

A total of 1090 trap nights was conducted at Lake One during periods in August and October of 1977, 1978, and 1979. No wolves were caught,

Table 4. Capture effort by helicopter for wolves collared in Wood Buffalo National Park, February 1978 to February 1980.

Month	Hours[1]	No. wolves	Hours/wolf
1978			
February	16.6	11	1.5
March	15.9	9	1.8
December	5.2	0	-
1979			
January	20.5	5	4.1[2]
March	19.8	10	2.0
December	2.3	2	1.2
1980			
February	1.8	3	0.6
Total	82.1	40	2.1

[1]Includes ferry time from Fort Smith to study area.
[2]Problems related to unsuitable pilot.

however, nine foxes (Vulpes vulpes), seven skunks (Mephites mephites), two lynx (Lynx canadensis), and two black bears (Ursus americanus) were trapped.

Capture success when using helicopters was greatly influenced by the pilot's ability to manoeuvre the helicopter in such a way that the target wolf could be kept in view at all times and be guided effectively into open terrain where the shooter could dart the wolf. Unfortunately the pilot available in early winter 1978-79 was inexperienced and unsuitable for this type of flying. We eventually contracted a Bell J-42 helicopter and pilot from Edmonton to do the flying in March 1979, and capture success increased dramatically (Table 4).

Unlike the Alouette II helicopter used earlier, it was possible to remove the door from the J-42, which made tracking and darting the wolves much easier. The Bell 206B likewise had better visibility for the shooter, in that the entire window on the shooter's side could be removed. A combination of a talented pilot, good visibility, experienced personnel, and luck resulted in a much lower time expenditure for wolves captured in 1979-80.

Sex and age ratios of captured wolves (Table 5) were 21 females:22 males, and 27 adults:16 immature wolves (less than 21 months). Colour phases were 15 black, 12 grey, 11 blonde, and 4 brown wolves (Appendix 1). The average weight of adults was 44 kg and 35 kg for immature wolves.

Wolves in this study were captured in late winter, when pups were large and difficult to identify. Wolves not readily distinguished as pups or yearlings were pooled as immature wolves.

Table 5. Sex and age distribution of 43 wolves captured in Wood Buffalo National Park, 1977 to 1981.

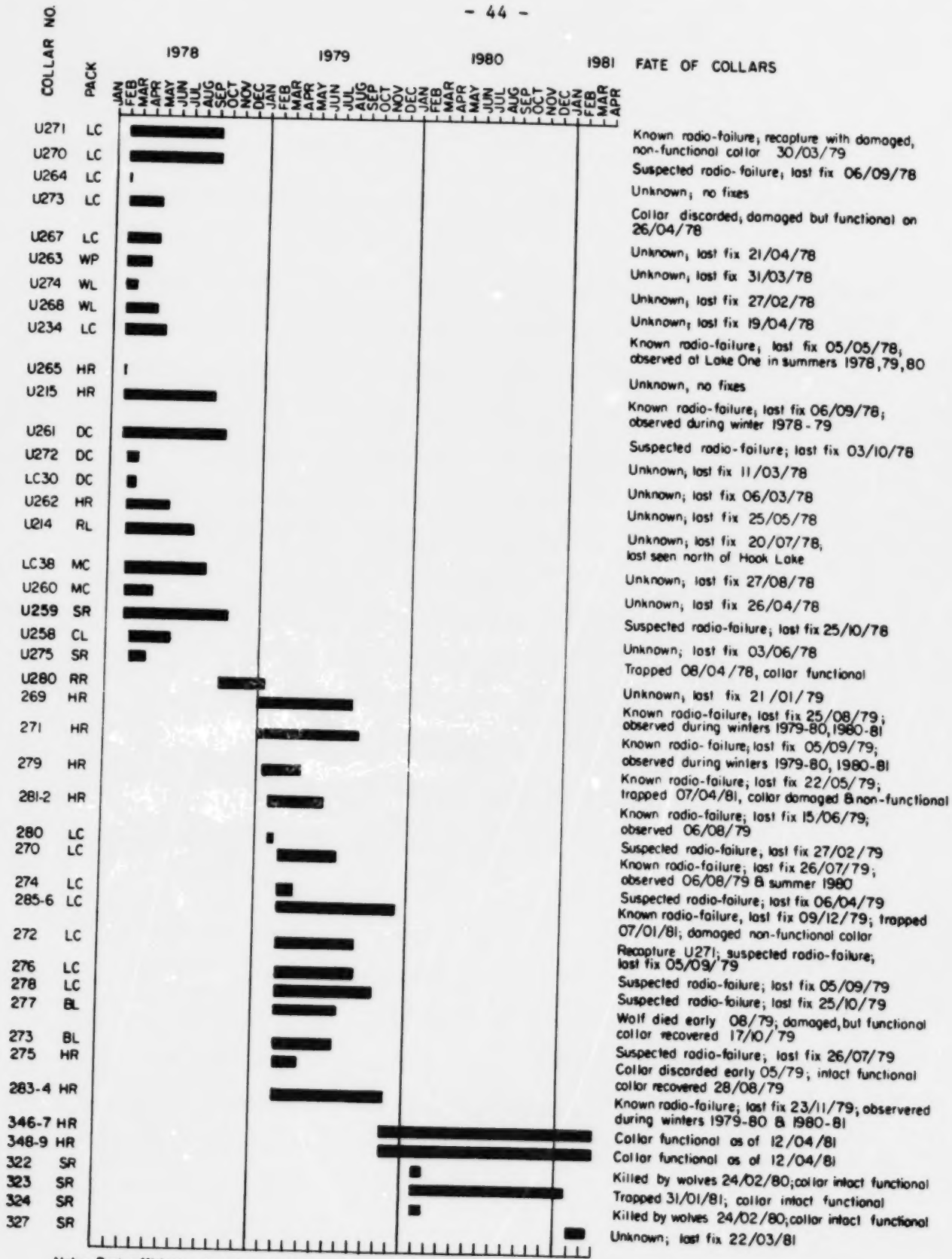
Year	Number of wolves examined	Adults		Immature	
		Males	Females	Males	Females
1977-78	21	7	6	3	5
1978-79	16	8	4	2	2
1979-80	5	2	-	-	3
1980-81	1	-	-	-	1
Totals	43	17	10	5	11

Other studies in which wolves were captured by helicopter are few, and the age ratios of captured wolves appear to vary with the status of the wolf population sampled. Ballard et al. (1981) reported that 52% (n = 103) of wolves captured in an exploited Alaskan population were less than two years old. Wolves captured and shot from a helicopter during 1977 and 1978 on bison ranges north of Wood Buffalo National Park (Van Camp, pers. comm.) were primarily adults (84%, n = 24); this population was believed to be declining at the time.

Results from northern Minnesota (Van Ballenberghe et al. 1975) and Riding Mountain National Park (Carbyn 1980) suggested that leg-hold trapping selects for young wolves in areas of high trapping pressure, although the former felt that a 69% immature segment of trapped animals in the fall was a realistic estimate of their abundance in the population.

Although adult males outnumbered adult females almost two to one in our study, the reverse was true for immature wolves (Table 5). The sex ratio of all captured wolves (21 females:22 males) was similar to sex ratios for wolves in northern Minnesota (Van Ballenberghe et al. 1975), though, the majority of the literature suggests that males predominate in wolf populations (Stenlund 1955; Kuyt 1972; Mech 1975; Fuller and Keith 1980). Mech (1975) speculated that males tended to be more common in food-stressed, high-density wolf populations, while females might be more abundant in wolf populations with high mortality rates. Assuming a 1:1 female to male ratio at birth, our data suggest that in Wood Buffalo National Park female wolves experienced lower mortality rates than males as young animals, but became more vulnerable as adults.

In 1978, 21 radio collars were used (Fig. 9). Radio signals from collars averaged 89 days in duration. Two of the instrumented wolves were


COLLAR NO.
PACK
1978
1979
1980
1981
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR
FATE OF COLLARS
U271 LC
U270 LC
U264 LC
U273 LC
U267 LC
U263 WP
U274 WL
U268 WL
U234 LC
U265 HR
U215 HR
U261 DC
U272 DC
LC30 DC
U262 HR
U214 RL
LC38 MC
U260 MC
U259 SR
U258 CL
U275 SR
U280 RR
269 HR
271 HR
279 HR
281-2 HR
280 LC
270 LC
274 LC
285-6 LC
272 LC
276 LC
278 LC
277 BL
273 BL
275 HR
283-4 HR
346-7 HR
348-9 HR
322 SR
323 SR
324 SR
327 SR
Known radio-failure; recapture with damaged, non-functional collar 30/03/79
Suspected radio-failure; last fix 06/09/78
Unknown; no fixes
Collar discarded, damaged but functional on 26/04/78
Unknown; last fix 21/04/78
Unknown; last fix 31/03/78
Unknown; last fix 27/02/78
Unknown; last fix 19/04/78
Known radio-failure; last fix 05/05/78; observed at Lake One in summers 1978,79,80
Unknown, no fixes
Known radio-failure; last fix 06/09/78; observed during winter 1978-79
Suspected radio-failure; last fix 03/10/78
Unknown, last fix 11/03/78
Unknown; last fix 06/03/78
Unknown; last fix 25/05/78
Unknown; last fix 20/07/78, last seen north of Hook Lake
Unknown; last fix 27/08/78
Unknown; last fix 26/04/78
Suspected radio-failure; last fix 25/10/78
Unknown; last fix 03/06/78
Trapped 08/04/78, collar functional
Unknown; last fix 21/01/79
Known radio-failure; last fix 25/08/79; observed during winters 1979-80, 1980-81
Known radio-failure; last fix 05/09/79; observed during winters 1979-80, 1980-81
Known radio-failure; last fix 22/05/79; trapped 07/04/81, collar damaged & non-functional
Known radio-failure; last fix 15/06/79; observed 06/08/79
Suspected radio-failure, last fix 27/02/79
Known radio-failure; last fix 26/07/79; observed 06/08/79 & summer 1980
Suspected radio-failure; last fix 06/04/79
Known radio-failure, last fix 09/12/79; trapped 07/01/81; damaged non-functional collar
Recapture U271; suspected radio-failure; last fix 05/09/79
Suspected radio-failure; last fix 05/09/79
Suspected radio-failure; last fix 25/10/79
Wolf died early 08/79; damaged, but functional collar recovered 17/10/79
Suspected radio-failure; last fix 26/07/79
Collar discarded early 05/79; intact functional collar recovered 28/08/79
Known radio-failure; last fix 23/11/79; observered during winters 1979-80 & 1980-81
Collar functional as of 12/04/81
Collar functional as of 12/04/81
Killed by wolves 24/02/80; collar intact functional
Trapped 31/01/81; collar intact functional
Killed by wolves 24/02/80; collar intact functional
Unknown; last fix 22/03/81

Note: Pack affiliation based on location of capture = LC-Lake Claire, HR-Hornaday River, SR-Salt River, BL-Baril Lake, WP-Willow Point, WL-Welstead Lake, DC-Darough Creek, RL-Roup Lake, MC-Murdock Creek, CL-Conibear Lake, RR-Rocher River

Figure 9. Monitoring duration and fate of collars placed on wolves in Wood Buffalo National Park, February 1978 to April 1981.

never relocated, and one wolf was monitored for a maximum of 228 days. None of the radio collars, except 11280, were monitored after 25 October 1978.

Radio collars placed on wolves during the second winter (1978-79) were monitored for an average of 145 days, and ranged from 10 to 257 days. As in 1978, no instrumented wolves could be monitored into the next winter. Collars placed on wolves in the third year (1979-80) continued to function throughout that winter, the summer of 1980, and the winter of 1980-81 as well. Two of these were operational as of 19 June 1981 and have been on the air for at least 527 days (75 weeks).

The average "field-life" for radio transmitters known or suspected to have failed was 184 days in 1978 (6 collars) and 155 days in 1979 (13 collars). There was no transmitter failure in collars applied in 1979-80. Collars placed on the Salt River pack (3) were all recovered and functional; wolf 323 carried its transmitter for 346 days from 18 February 1980 to 31 January 1981 (Fig. 9) when it was trapped. Two wolves in the Hornaday River pack carried double transmitter collars from 1 December 1979 until April 1981 and possibly beyond that date.

Local interference in the 150-51 MHz range made monitoring extremely difficult during 1978, and from the limited data it was not possible to pinpoint any one reason for loss of radio signals. We tentatively concluded that radio interference, dispersal of wolves and transmitter failure were contributory causes.

By switching to a frequency of 171-72 MHz during the winter of 1978-79, we were able to eliminate extraneous signals and determine more accurately the reasons for signal loss. Although in 1978 four transmitters

were suspected to have failed, only one wolf was observed to be carrying a nonfunctional transmitter. However, a recapture in 1979 together with more intensive monitoring and observations of wolves in 1979 and 1980 confirmed that the most radio-signal losses were due to transmitter failure. Of the 15 radio collars applied in the winter of 1978-79, seven were known to have failed by late summer, and another six were suspected to have failed. Two functional transmitters were recovered during the summer.

Known transmitter failures were either determined from nonfunctional transmitters on wolves recaptured or killed by trappers, or from observations of wolves carrying collars that were not transmitting (Table 6). The fate of the six of eight collars placed on the Hornaday River pack, monitored intensively for three winters, was determined by observations of instrumented wolves in subsequent winters. Five of the six failed within the first year of application; the other was discarded by the wolf and recovered intact. The fact that at least two (269, 271) of the wolves collared in the Hornaday River pack were pack members from at least 1979 to 1981 suggested that dispersal was not an important factor in the loss of radio signals. Although the Lake Claire pack was not monitored intensively, abrupt signal losses and subsequent observations of collared wolves with nonfunctional transmitters also indicated a high rate of transmitter failure (Fig. 9).

Dispersal of wolves, especially in 1978 when monitoring capability was limited, cannot be entirely discounted. In at least two instances in 1978, instrumented wolves moved large distances (50 km or more) between subsequent radio locations before their signals were lost. One wolf was eventually located near Hook Lake, Northwest Territories, 120 km north of

Table 6. Condition of radio-collars recovered, or observed on wolves captured in Wood Buffalo National Park from 1978 to 1980.

	Circumstance	Wolf collar #	Damaged	Not damaged	Functional	Non-functional
On wolf more than 6 months						
	Recapture	U271	*			*
	Trapped	279	*			*
	Trapped	285-6	*			*
	Died (?)	277	*		*	
	Trapped	323[1]		*	*	
	Live observation	269	*			*
	Live observation	271	*			*
On wolf less than 6 months						
	Discarded collar	U273	*		*	
	Trapped	U275		*	*	
	Discarded collar	275		*	*	
	Killed	322[1]		*	*	
	Killed	324		*	*	

[1]Radio-collars constructed by Canadian Wildlife Service during 1979-80 were reinforced with fibreglass; none of those were damaged and all were functional.

where it had last been seen. Van Camp and Gluckie (1979) reported the long-distance movement (670 km) of a wolf captured in the Hook Lake area and killed several months later near Cold Lake, Alberta. However, careful monitoring procedures in 1979, when signal interference was eliminated and the effective monitoring range increased dramatically, suggested that transmitter failure was the primary cause of signal loss.

Four of five collars that were examined from wolves which had carried them for at least six months, had been damaged. Such damage was determined by evidence of tearing of the collar band and/or tooth marks on the acrylic transmitter assembly. Three of the four collars were nonfunctional (Table 6). Two other wolves observed from the air and on the ground, were missing transmitter assemblies as indicated by a dangling collar band. It is conceivable that damage inflicted by wolves on radio collars comes from other members of the pack, perhaps during times of intense social interaction such as at dens and at rendezvous sites; many of the signals disappeared during mid to late summer. This source of transmitter failure has also been documented in Minnesota (Thiel and Fritts 1983) but not for Manitoba (Carbyn 1980).

2. Pack size, organization and dynamics in winter

Thirty-eight instrumented wolves in eight packs of three or more animals, and five wolves captured as lone wolves or pairs were radio tracked for periods of several days to 75 weeks. The number of groups monitored after 1979 was less due to more intensive tracking of the Hornaday River pack for purposes of behavioural studies and determining predation rates.

The mean number of wolves in two instrumented packs (the Hornaday River and Lake Claire packs) was 11 from winters 1977-78 to 1980-81 (Table 7). Mean pack sizes in Area I and II combined, (excluding single wolves and pairs) observed on bison surveys, ranged from a high of 14.5 wolves in 1973-74 to a low of 6.0 wolves in 1975-76 and 1978-79 (Table 8).

The frequency distribution of population units (lone wolves, pairs, and packs) for all aerial observations in winters 1970-71 to 1980-81 (n = 318) is shown in Figure 10. Mean pack size during this time was 9.2 wolves (Table 9). The proportion of observations of single wolves and pairs respectively varied from a low of 11.8% in 1970-71 and 6.1% in 1971-72, to a high of 52.6% in 1975-76 and 30.4% in 1976-77 (Fig. 11).

Data on pack size in Wood Buffalo National Park (Table 9, Fig. 10) generally agree with those suggested by most of the literature, in that wolf pack size varies greatly, but seven to eight members seem to be most common. A count of 42 wolves on the northwest shore of Lake Claire on 20 February 1974 (Fau and Tempany 1976) is the largest reliably recorded number of wolves in "one pack". It was not clear from the observation if possibly the pack was made up of several family units from one area. Other large "packs" exceeding 20 wolves were observed on several occasions that winter. Mech (1970) outlined a theory of pack formation based on social bonding between one mated pair and their offspring of two consecutive years to explain the usual 7-8 member pack, or larger numbers if survival of offspring was higher. It is possible that an increase in the number of observations of 17-18 member packs (Fig. 10) indicated the presence of two breeding units with offspring, and larger packs were the result of a combination of multiple breeding and high survival rates.

Table 7. Maximum numbers of wolves observed in packs in early, mid, and late winters 1977-78 to 1980-81 in primary bison ranges of Wood Buffalo National Park.

Year	Location	Pack designation	Maximum pack size observed[1]		
			Early winter (Nov.-Dec.)	Midwinter (Jan.-Feb.)	Late winter (Mar.-Apr.)
1977-78	Lake Claire	Lake Claire	14g	13	11
	Welstead Lake	Welstead Lake			8
	Baril Lake	Baril Lake		9	
	Hay Camp/Darough Creek prairies	Hornaday River		8	8
	Darough Creek prairies	?			5
	Murdock Creek meadows	Murdock Creek			10
	Point Providence	Point Providence	9		
	Salt Plains	Salt River	13g		3
1978-79	Lake Claire	Lake Claire		12	16
	Revillon Coupe	?		7	
	Baril Lake	Baril Lake	8	7	6
	Hay Camp/Darough Creek prairies	Hornaday River	14	14	10
	Murdock Creek meadows	Murdock Creek	11		8
	Salt River	Salt River		5	
1979-80	Baril Lake	Baril Lake		6	
	Mamawi Lake	Mamawi Lake		9g	
	Hay Camp/Darough Creek prairies	Hornaday River	12	14	12
	Murdock Creek meadows	?		4g	
	Point Providence	Point Providence	7	7	
	Salt Plains	Salt River	6	7	
1980-81	Lake Claire	Lake Claire		9g	
	Baril Lake	Baril Lake		9g	
	Hilda Lake	?			9g
	Birch River	?		8	
	Hay Camp/Darough Creek prairies	Hornaday River	7	9	8
	Murdock Creek meadows	?		6t	
	Salt Plains	Salt River	7		

[1]All aerial observations except where noted.
g = ground observation
t = track evidence

Table 8. Aerial observations of non-instrumented wolves on regular bison surveys in primary bison ranges of Wood Buffalo National Park; winters 1970-71 to 1980-81 (from Park Warden Service files).

Year	Hours flown	Number wolves sighted	Number wolves sighted /hour	Number wolf units observed				
				Single wolves	Pairs	Packs	Mean pack size	Range
AREA I								
1970-71	-	26	-	0	1	3	8.0	4-14
1971-72	-	87	-	2	0	8	10.6	4-17
1972-73	78.4	110	1.4	11	5	13	6.8	3-13
1973-74	36.0	53	1.5	3	1	5	9.6	6-20
1974-75	47.0	81	1.7	2	1	11	7.0	3-14
1975-76	23.6	35	1.5	4	1	4	7.3	3-13
1976-77	34.4	50	1.4	3	3	7	5.9	4-99
1977-78	30.5	10	0.3	1	0	1	9.0	
1978-79	23.7	18	0.8	0	0	3	6.0	3-10
1979-80	26.2	18	0.7	0	0	2	9.0	8-10
1980-81	15.0	5	0.3	0	0	1	5.0	
Area II								
1970-71	34.5	93	2.7	2	2	9	9.7	4-19
1971-72	-	172	-	4	1	18	9.2	3-20
1972-73	61.3	337	5.5	6	3	28	11.6	3-28
1973-74	62.9	308	4.9	9	7	18	15.8	3-42
1974-75	46.5	84	1.8	9	3	7	9.9	3-17
1975-76	39.7	19	0.5	4	1	3	4.3	3-7
1976-77	43.2	53	1.2	2	4	4	10.8	7-15
1977-78	33.3	21	0.6	3	2	2	7.0	5-9
1978-79	31.6	18	0.6	4	1	2	6.0	5-7
1979-80	20.5	20	1.0	0	0	2	10.0	9-11
1980-81	12.7	13	1.0	2	0	2	5.5	3-8
Area I and II combined								
1970-71	-	-	-	2	3	12	9.3	4-19
1971-72	-	-	-	6	1	26	9.6	3-20
1972-73	139.7	447	3.2	17	8	41	10.1	3-28
1973-74	98.9	361	3.7	12	8	23	14.5	3-42*
1974-75	93.5	165	1.8	11	4	18	8.1	3-17
1975-76	63.3	54	1.9	8	2	7	6.0	3-13
1976-77	77.6	103	2.3	5	7	11	7.6	4-15
1977-78	63.8	31	0.5	4	2	3	7.7	5-9
1978-79	55.3	36	0.7	4	1	5	6.0	3-10
1979-80	46.7	38	0.8	0	0	4	9.5	8-11
1980-81	27.7	18	0.6	2	0	3	5.3	3-8

*Exact social status of this grouping was not known.

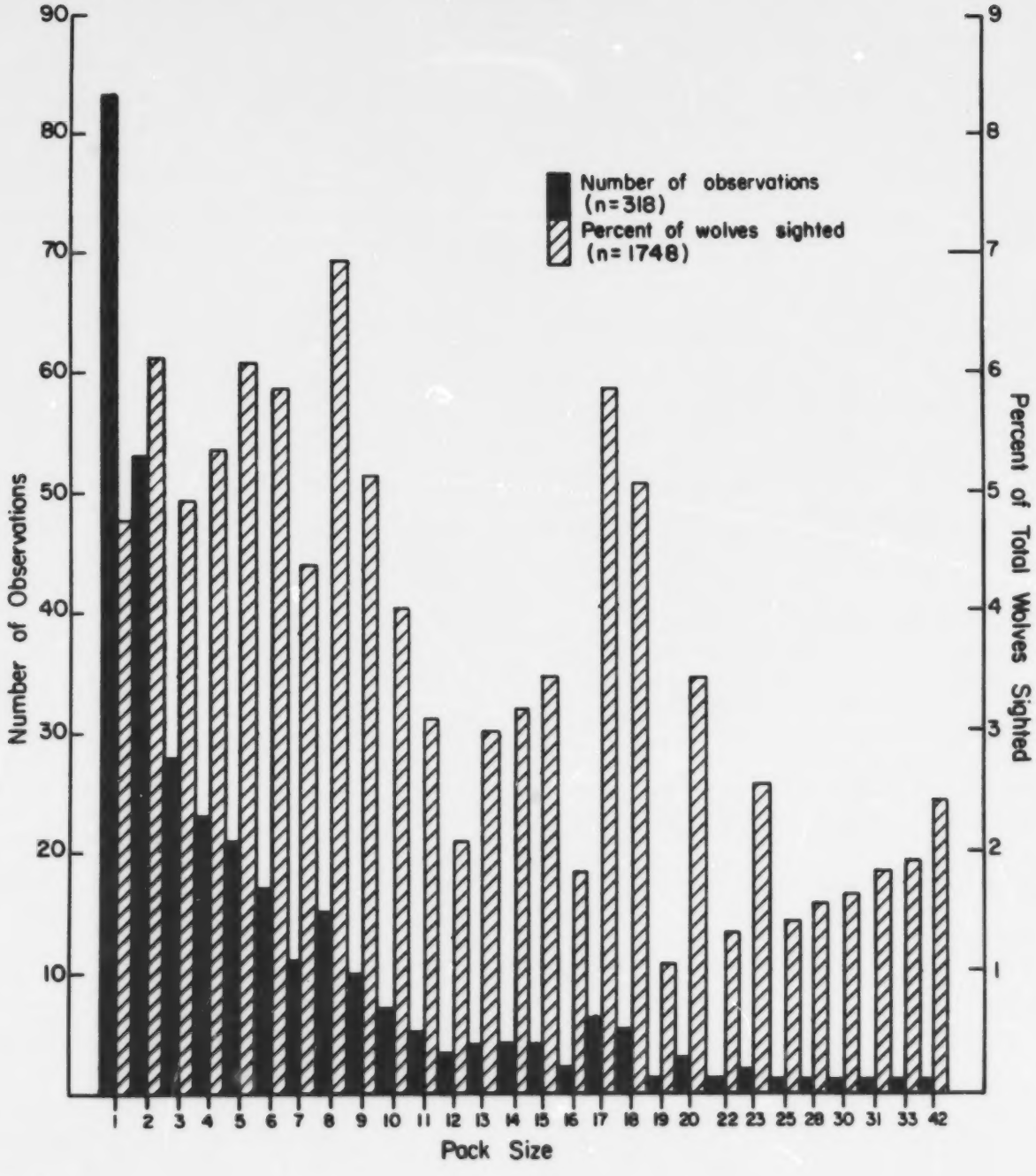


Figure 10. Frequency distribution of wolf population units, determined from all aerial observations of non-instrumented wolves in primary bison ranges of Wood Buffalo National Park; winters 1970-71 to 1980-81.

Table 9. Aerial observations of non-instrumented wolves on all surveys and flights in primary bison ranges of Wood Buffalo National Park; winters 1970-71 to 1980-81.

Year	Area I						Area II						Area I and II combined					
	Single wolves	Pairs	Packs	Mean pack size	Range	Total wolves	Single wolves	Pairs	Packs	Mean pack size	Range	Total wolves	Single wolves	Pairs	Packs	Mean pack size	Range	Total wolves
1970-71	0	1	3	8.0	4-14	26	2	2	9	9.7	4-19	93	2	3	12	9.3	4-19	119
1971-72	2	0	8	10.6	4-17	87	4	2	17	9.9	3-20	174	6	2	25	10.0	3-20	261
1972-73	11	5	13	6.8	3-13	110	6	3	30	11.7	3-28	363	17	8	43	10.2	3-28	473
1973-74	3	1	5	9.6	6-20	53	9	7	18	15.8	3-42	308	12	8	23	14.5	3-42	361
1974-75	2	1	11	7.0	3-14	81	9	3	7	9.9	3-17	84	11	4	18	8.1	3-17	165
1975-76	4	1	4	7.3	3-13	35	6	1	3	4.3	3-7	21	10	2	7	6.0	3-13	56
1976-77	3	3	7	5.9	4-9	50	2	4	4	10.8	7-15	53	5	7	11	7.6	4-15	103
1977-78	2	2	5	6.3	3-10	44	6	4	7	4.6	3-9	46	8	6	13	5.4	3-10	90
1978-79	0	0	8	8.1	3-14	65	7	3	8	6.8	5-11	67	7	3	16	7.4	3-14	132
1979-80	0	1	3	8.3	7-10	27	4	0	5	6.0	3-11	34	4	1	8	6.9	3-11	61
1980-81	1	2	3	6.0	5-7	23	4	0	6	4.5	3-8	30	5	2	9	4.8	3-8	53
Total	28	17	71	7.6	3-20	601	59	29	114	10.1	3-42	1273	87	46	185	9.2	3-42	1874

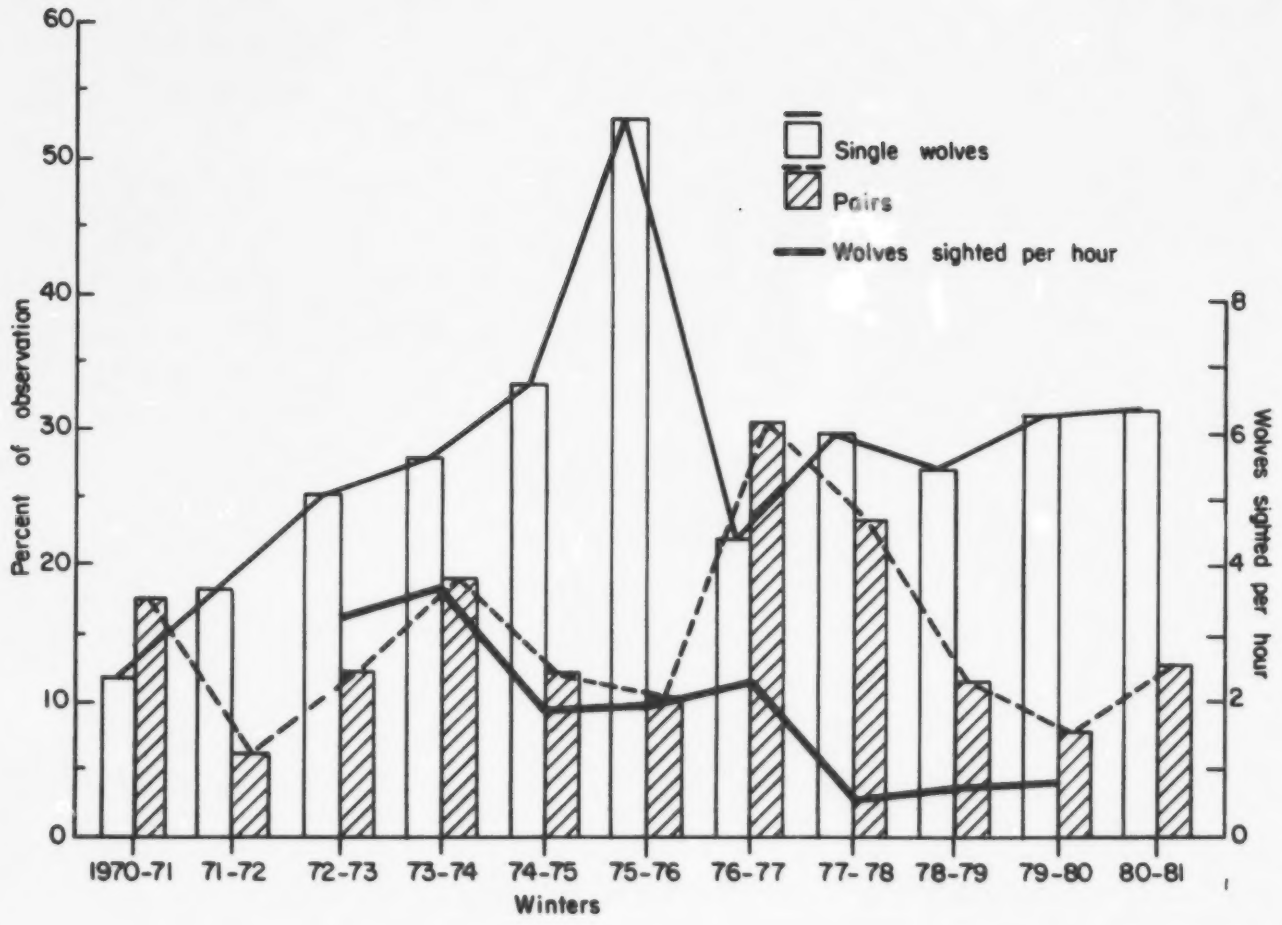


Figure 11. Aerial observations of non-instrumented single wolves and pairs, and number of wolves sighted per hour on regular bison surveys in primary bison ranges of Wood Buffalo National Park; winters 1970-71 to 1980-81.

Although one litter per pack is considered most common (Van Ballenberghe and Mech 1975; Peterson 1977), multiple litters were recorded by Murie (1944), Rausch (1967), Clark (1971), and Haber (1977). Carbyn (1980a) felt that multiple litters could occur if abundant food was available and mortality rates were low; packs of 20-25 wolves prior to 1975 in Riding Mountain National Park were thought to have resulted from high survival and possible multiple sets of offspring.

a. Peace-Athabasca delta

Pack confirmation in the delta was not clearly defined. It is an area of high prey density with marked seasonal shifts of the bison herds. Our studies have not adequately defined the social structure of the wolf population in the delta. However, some interesting observations were made and, because they could shed light on future studies, descriptions are discussed below. During late February 1978 six members of a pack of at least 14 wolves (D. West, pers. comm.) were captured on the northwest shore of Lake Claire (Fig. 12). From 20-23 February this pack consisted of at least three subgroups of seven, three, and three wolves. On 20 February two wolves, males U270 and U271, were captured from the group of seven. The following day this group was located 5 km east of the North Arm, where female U264 was captured. On 22 February, three unmarked wolves were located in Sweetgrass Creek Bay, and three others on the west side of Lake Claire; two wolves (male U273, female U267) were captured at the latter location near a fresh bison kill. Wolves U270 and U264 were located west of Sweetgrass Island. The following day at least five wolves (not identified) were spotted at the same kill, and one more wolf, female U234, was captured.

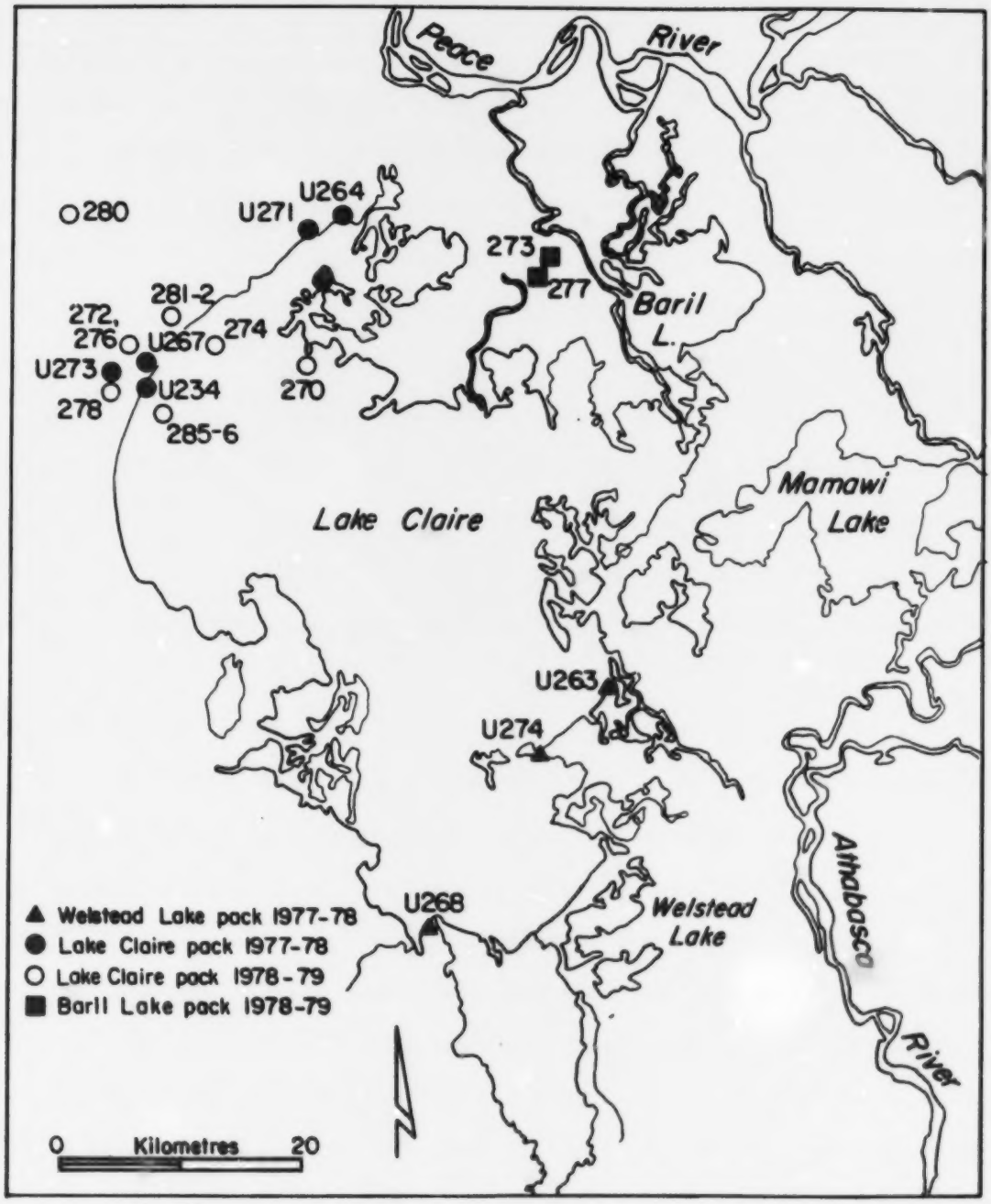


Figure 12. Capture locations of instrumented wolves on primary bison ranges south of the Peace River, Wood Buffalo National Park; 1977-78 and 1978-79.

Between 20 February and 25 April, three wolves (males U270, U271 and U273) were always observed alone or separately with unmarked associates (n = 14 observations). The remaining wolves captured near Lake Claire were relocated sporadically and for a short duration. Female U264 was never relocated. Two locations on female U267 indicated movements of over 90 km. Before the signal was lost in early May, female U234 was relocated three times about 20 km from her capture site.

An immature male (U263) travelling alone in the vicinity of Hilda Lake (Fig. 12) when captured on 22 February, was observed alone twice on 27 February and 31 March, and associated once with male U271 and four other wolves on 29 March before its signal was lost.

Two wolves were captured out of a group of three traveling along the southeast shore of Lake Claire on 22 February. Radio contact was lost with female U274 within a week, but male U268 was observed with a pack of seven (11 March) and five (22 March) wolves, and was observed alone on 27 February and 1 April.

In 1979, two wolves (male 281-2, female 280) were captured out of a pack of 11-16 during the week of 22-27 January on the north shore of Lake Claire (Fig. 12). Female 280 was relocated three times before its signal was lost sometime after 27 February. Male 281-2 and six others, including recapture male U271, captured in late March (Fig. 12), were relocated at irregular intervals until late April. Unlike the previous winter, instrumented wolves were always located together (n = 14 observations), and the pack remained a cohesive unit into May (Table 10). Two other wolves (males 273, 277) were captured on 30-31 March out of pack of seven near

Table 10. Identification and maximum size of estimated different social units of wolves observed on primary bison ranges in Wood Buffalo National Park; winter 1977-78.

Social unit	Maximum numbers observed	Date	Source
Hornaday River pack[1]	8	16/03/78	Radiotelemetry observation
Darough Creek pack[1]	5	16/03/78	Radiotelemetry observation
Murdock Creek pack[1]	10	01/03/78	Wolf reconnaissance survey observation
Salt River pack[1]	3	31/03/78	Radiotelemetry observation
Raup Lake duo[1]	2	24/04/78	Radiotelemetry observation
Point Providence pack	9	02/11/77	Bison survey observation
Lake Claire pack[1]	14	08/12/77	Ground tracking observation
Baril Lake pack	9	16/01/78	Bison survey observation
Manawi Lake pack	4	20/02/78	Ground tracking observation
Hilda Lake pack	5	16/03/78	Bison survey observation
Welstead Lake pack[1]	8	11/03/78	Radiotelemetry observation
Birch River pack	8		Estimate, based on bison survey observation in 1981-81.

[1]Instrumented units.

Baril Lake (Fig. 12) and observed twice as part of the same unit between 1 and 29 April.

b. Area I primary bison ranges

Observation of packs and radiotelemetry data north of the Peace River during 1978 were minimal primarily due to radio transmitter failure and interference problems. Wolves captured in the Hay Camp-Darough Creek prairies during late winter 1978 possibly belonged to two distinct packs which both traveled in the same area (Table 11).

Three wolves were captured out of a pack of 7-8 in the vicinity of the Hornaday River (Fig. 13) in late February (male U215, female U265) and early March (female U262). Female U265 was never relocated, while male U215 and female U262 during April-May were associated with a denning pack in the Hay Camp prairies. Three wolves (males U261, LC30; female U272) were captured out of a pack of five in the Darough Creek prairies on 2 March (Fig. 13). Radio contact was lost with this group a week after placement of collars, so it was not possible to determine its relation to the other pack.

Two immature wolves (male U260, female LC38) were captured out of a pack of 10 in the Murdock Creek area on 7 March (Fig. 13). Male U260 was relocated twice in groups of four and seven wolves in the general vicinity of its capture site in late Mrch before its signal disappeared. Female LC38 was observed once 18 April by itself in the Canadian Shield country east of the Slave River about 35 km from its capture site. Female U214, traveling alone when captured near Raup Lake (Fig. 13) on 6 March, was observed once with another wolf on 26 April before traveling north out of the park in early summer.

Table 11. Summary of wolf observations on primary bison ranges in Wood Buffalo National Park, winters 1977-78 to 1980-81, as they relate to pack splitting and home range overlap.

Date(s)	Location	Observations
02/02-30/04/78	Peace-Athabasca delta	Members of Lake Claire pack (14 wolves in early December 1977) separated into at least 3 sub-units along north shore of Lake Claire. Males U270, U271 dispersed into separate denning areas.
22/02-11/03/78	Peace-Athabasca delta	Single male U263 observed with male U271 and part (6 wolves) of Lake Claire pack.
27/02-21/04/78	Peace-Athabasca delta	Lake Claire pack member female U267 located 40 km west, then 50 km east of capture site.
22/02-11/03/78	Peace-Athabasca delta	Male U268 captured as part of a trio; later observed as part of a pack of 7 near Welstead Lake.
24/02-11/03/78	Hay Camp/Darough Creek prairies	Overlap in home range of two possibly related units of 8 and 5 wolves.
01/03-18/04/78	Murdock Creek meadows	Reduction in observed pack size of Murdock Creek pack from 10 to 7 wolves between 1 and 11 March. Murdock Creek pack member female LC38 alone 35 km east of capture site on 18 April.
06/03-20/07/78	Raup Lake	Lone female U214 relocated in late July 160 km north of capture site with 3 unmarked wolves.
27/02/79	Hay Camp area	Tracks of 3-4 wolves near Hay Camp within the home range of the Hornaday River pack.
03-15/03/79	Hay Camp/Darough Creek prairies	Hornaday River pack member male 271 observed alone; rest of pack (10 wolves) split into at least two sub-units.
21-23/03/79	Hay Camp/Darough Creek prairies	Single wolf following tracks of the Hornaday River pack.
26/03-01/04/79	Hay Camp area	Pack of 6, 8 wolves sighted on the Slave River east of Hay Camp.
06-11/04/79	Hay Camp/Darough Creek prairies	Hornaday River pack member male 283-4 and 4 other wolves separated from rest of the pack.
27/02/81	Lynx Lake	Pack of 5 wolves in southwest corner of Hornaday River pack's winter home range.

Table 11. Continued.

Date(s)	Location	Observations
29/12/79-?	Hay Camp/Darough Creek prairies	Hornaday River pack split into at least two sub-units of 2 and 9 wolves.
22-31/01/80	Hay Camp area, Murdock Creek meadows, Area II	Hornaday River pack split into two sub-units of of 2 and 12 wolves; the main pack travels into the Murdock Creek meadows and Area II 100 km south of Hay Camp.
18-24/02/80	Hay Camp Prairies	Group of 7-8 wolves (Salt River pack) kill bison within the home range of the Hornaday River pack and is later attacked by the Hornaday River pack.
23-25/03/80	Hay Camp prairies	Two unmarked wolves near Salt River pack male 323; all within the Hornaday River pack's home range.
30-31/03/80	Raup Lake meadows	Hornaday River pack at densite suspected to have been occupied by the Salt River pack in 1979, 40 km northwest of Hay Camp.
Summer 1980	Hay Camp/Darough Creek prairies	Suspected major split in Hornaday River pack partially due to dispersal of alpha male possibly into Murdock Creek meadows in late February 1980.
12/11/80-22/ 01/81	Hay Camp/Darough Creek prairies	Salt River male 323 joined with male 283-4 (alpha male of Hornaday River pack in 1978-79) plus an unmarked wolf and spent much of December and January within home range of Hornaday River pack.
31/12/80-21/ 01/81	Hay Camp Darough Creek prairies	Hornaday River pack member female 348-9 separated with 3 other wolves from main pack of 6.
15-18/02/81	Hay Camp/Darough Creek prairies	Single wolf near Hornaday River pack.
22/02/81	Hay Camp/Darough Creek prairies	Two non-associated wolves retreat from Hornaday River pack; a single wolf 3 km north of pack.
26/03-04/04/81	Hay Camp/Darough Creek prairies	Hornaday River pack member female 346/7 separated from main pack.
05/04/81	Salt River	Hornaday River pack member female 279 (1978-79) snared 50 km north of capture site.

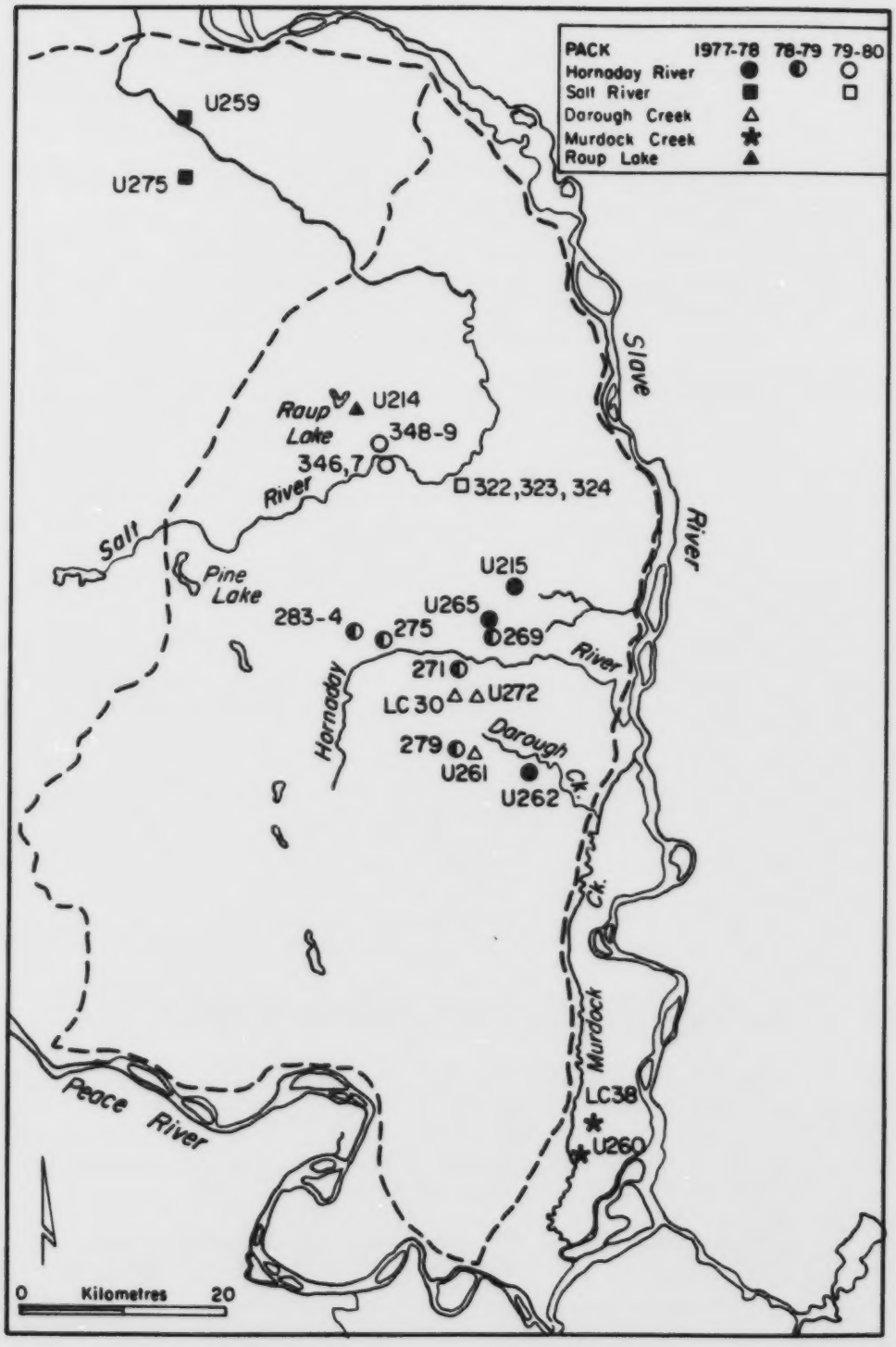


Figure 13. Capture locations of instrumented wolves north of the Peace River, Wood Buffalo National Park; winters 1977-78, 1978-79, and 1979-80.

A pack of 10-13 wolves was heavily trapped in the Salt Plains area on the northeast edge of the park during the winter of 1977-78 by a local resident (D. Dragon, pers. comm.). An immature wolf (male U259) was found unharmed in a snare on 12 March, instrumented and released. This wolf was relocated with another wolf on 31 March, the latter (female U275) was captured and instrumented on that date. Female U275 was killed in a snare on 8 April, while male U259 was monitored throughout the summer as a solitary wolf.

Due to lack of radio-tracking continuity, it was not possible to document changes in pack size over consecutive winters, except for wolves captured in the Hay Camp-Darough Creek prairies (Hornaday River pack), although in some cases observations of wolves, or their sign were used to estimate presence of packs in winters following 1977-78 (Table 7).

Information on pack size and dynamics for the Hornaday River pack in winters 1978-79, 1979-80 and 1980-81 were derived mainly from observations of instrumented wolves and their associates. Pack size during this time varied from 8-14 wolves in early to midwinter, and from 6-10 in late winter (Table 7).

In 1978-79, pack size decreased from 14 to 10 from early December to mid-February. Although mortality may have accounted for this decrease, observations of instrumented wolves indicated that splitting of the pack occurred. From 3-15 March and 6-11 April, the Hornaday River pack split into at least two groups. Male 271 traveled alone from 3-15 March; the remaining instrumented segment of the pack (females 269, 279) of six wolves, split off from the main pack of 10. The pack also separated briefly late in March and again from 6-11 April when male 283-4 split off with four others. Track and scat evidence indicated that 3-4 wolves (whose

affiliation was unknown) traveled within the winter range of the Hornaday River pack.

Observed pack size increased from 10 to 14 from early December to late January, 1979-1980, then decreased to 10 by early April. In late December the pack split into a least two groups, as the two instrumented wolves (females 346-7, 348-9) traveled together but separate from the rest of the pack. During late January the main pack (10-12 wolves) traveled south into the Peace-Athabasca delta, but at least two wolves, including female 346-7 remained in the Hay Camp-Darough Creek prairies. From mid-February on, pack size varied from 8-12 wolves.

Unlike 1978-79, when the pack was more cohesive, and a larger number of collared individuals made identification of pack members possible (Oosenbrug and Carbyn 1982), it was difficult to determine which wolves left and joined the pack during 1979-80. Records of colour phases in the pack indicated that most of the exchange of pack members seemed to involve black wolves (Oosenbrug et al. 1981).

Observations of the Hornaday River pack during winter 1980-81 suggested that a major splitting or reduction of the pack had occurred since the previous winter. Pack size remained constant from 6-7 wolves throughout December, although on 31 December female 348-9 had split off and joined an unidentified group of two others. This wolf rejoined the main group sometime before 21 January. From late January to early April pack size varied from 6-9 wolves. No splitting by instrumented wolves was observed until 26 March, when female 346-7 left the pack (6 wolves) and did not rejoin it until 4 April.

In each winter from 1978-79 to 1980-81 there was evidence of the presence of wolves apparently loosely associated with the Hornaday River pack. On 21 and 22 March 1979, a black wolf travelled on the trail 2-3 km behind the pack between kills. During late March 1980 two black wolves were observed near male 323, an abandoned member of the Salt River pack. The three wolves were within the composite winter range of the Hornaday River pack. From 15-18 February 1981 a black wolf was seen in close proximity, but not with the Hornaday River pack (7 wolves). The wolf fed on a bison carcass killed by the pack, but only after the pack had moved away from it. On 15 February this wolf ran away from the approaching pack and appeared "extremely nervous". On 22 February the pack was within 1 km of what seemed to be two non-affiliated wolves. Upon detecting the pack these two wolves ran in different directions away from the pack, which had not noticed the two. At the same time a single black wolf was observed three kilometres north of the two groups.

Information on pack size and dynamics of wolves in the Salt Plains area (Salt River pack) after 1977-78 were based primarily on observations of one surviving instrumented wolf in that pack. Male 323 traveled alone most of late winter 1980, after a confrontation between the Hornaday River and Salt River packs on 24 February reduced and dispersed the Salt River pack. After 24 February this wolf was observed with a pack of four wolves on 2 and 3 March, then traveled alone until 6 April, when it was associated with two unidentified wolves. From 12 November 1980 to 22 January 1981 it traveled with two other wolves, one of which (male 283-4) had been a dominant member of the Hornaday River pack during 1978-79. This trio spent

approximately 50% of its time within the home range of the Hornaday River pack during December and January.

Our radiotelemetry data suggested that splitting and reforming of wolf packs in winter was common throughout the primary bison ranges of the park. Information on the splitting of packs into subunits in winter has been recorded on Isle Royale (Jordan et al. 1967; Wolfe and Allen 1973), Alberta (Carbyn 1975), and Alaska (Haber 1977). These studies showed that splitting was relatively common and variable in frequency, and form. Haber (1977) believed that food availability was the prime determinant in the splitting of two wolf packs in Mount McKinley National Park. Other records of pack splitting come from Burkholder (1959) in Alaska, Mech and Frenzel (1971) in Minnesota and Carbyn (1975) in Alberta. Pimlott et al. (1969) reported the joining of what they thought were separate packs in Algonquin Provincial Park, Ontario, however as Haber (1977) noted, these observations probably represented splitting and recombination between subunits of the same pack.

In our study, evidence of mortality related to changes in pack size was sparse. Pack size in the Peace-Athabasca delta was smallest (Table 9), and incidence of single wolves largest (Fig. 11) during 1975-76, when trapping pressure was high in the delta and flooding conditions a year earlier had reduced the bison population by one-third. It is possible that flooding, disturbance (skidoo traffic) and trapping in the Peace Athabasca delta from 1974 to 1976 severely disrupted pack structure and reduced pack sizes. Trapping pressure north of the Peace River has not been intensive over the years, and changes here in occurrence of single wolves and pack sizes were less evident (Table 9).

3. Numerical trends and population estimates

Observations of wolves on bison surveys systematically recorded by the Warden Service since 1972 indicated that wolf numbers in the Peace-Athabasca delta (Area II) decreased from 1972 to 1977, and remained fairly constant north of the Peace River (Area I) during this time (Table 8).

It appeared that wolf numbers in the park and surrounding areas increased rapidly during the late 1960s and early 1970s. Wolves apparently declined dramatically in the Peace-Athabasca delta during 1974 and 1975, which may have resulted from increased harvesting in winters 1973-74 and 1974-75, and severe flooding conditions in the spring of 1974.

Although accurate figures on wolf harvests in the park are difficult to obtain (Loranger 1977), it is likely that high fur prices in 1974 and 1975 provided an incentive for local residents to take many wolves on traplines and by shooting. According to park reports approximately 200 wolves were killed by trappers in winter 1974-75 (Fau 1975). Most of the Peace-Athabasca delta was under 30 cm or more of water from May to September 1974, and most of the several thousand bison which drowned were never accessible to wolves (Cooper, pers. comm.). A reduced prey population, but more likely loss of suitable denning habitat may have resulted in poor reproductive success in 1974.

Estimates of the wolf population in the primary bison ranges were derived from aerial observations, ground observations and radiotelemetry information. These resulted in an estimate of 11 different social units and a total of 77 wolves (Table 10, Fig. 14). Eight wolves in a pack not observed in 1977-78 (Birch River pack), but which on the basis of observations prior to and after 1977-78 (Table 7), apparently occupied the

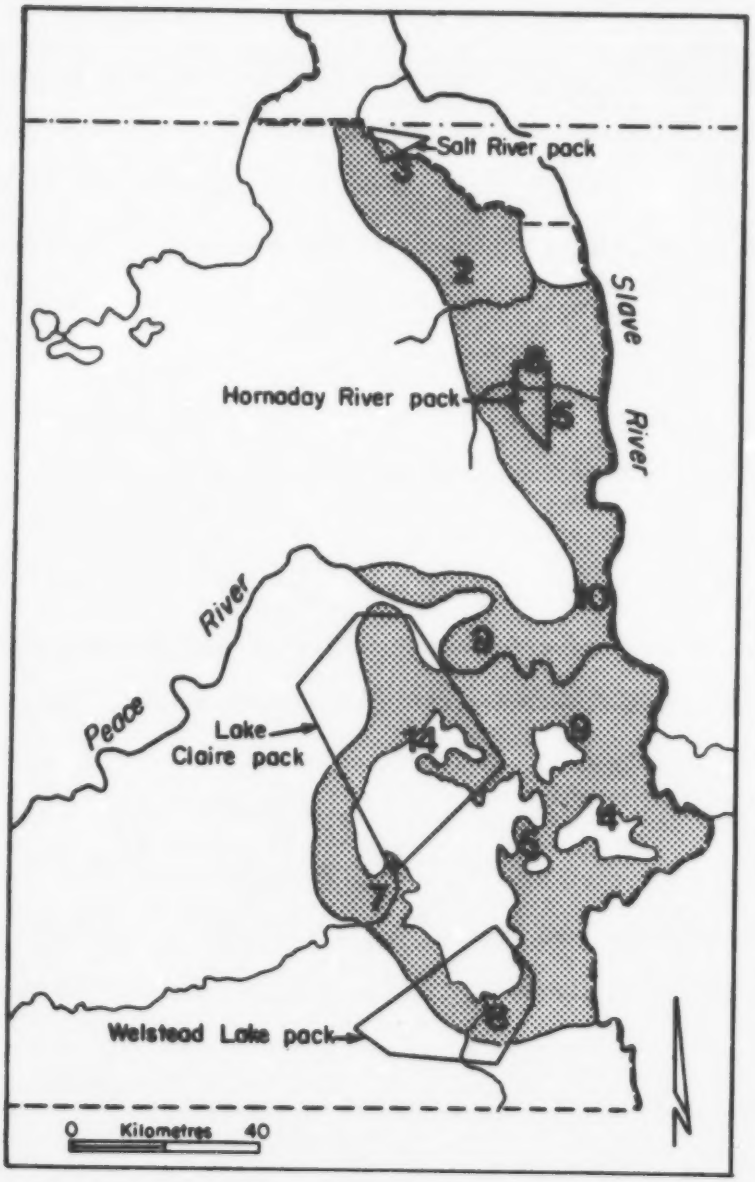


Figure 14. Location and maximum observed size of an estimated 11 different wolf packs observed in winter 1977-78, and home-range size of four instrumented packs radio-tracked in late winter 1978 on primary bison ranges of Wood Buffalo National Park.

extreme southwest portion of the primary bison ranges; these were included in the total estimate of 85 wolves. This estimate was considered a minimum figure. Observations relating to poorly defined pack structures and overlap in home ranges (Table 11) suggested the presence of other unidentified social units. Earlier workers (Pimlott et al. 1969, Mech 1973, Carbyn 1980; Fuller and Keith 1980, Fritts and Mech 1981) calculated wolf numbers on the basis of identified packs and added 10-20% for single wolves which presumably shared home ranges with packs.

The extrapolated population over the entire primary bison ranges was 136 wolves (including 12 single wolves). This calculation was based on data from four instrumented packs (33 wolves) which occupied 1465 km^2 (polygon-perimeter method) of the estimated 5500 km^2 of accessible habitat in the primary bison ranges of the park during the winter of 1977-78 (Fig. 14). Density values based on these estimates were one wolf per 40-65 km^2 in the primary bison ranges, and were lower than those in more southerly areas, but higher when compared to areas of similar latitude (Table 13).

4. Home ranges and dispersal patterns

The problem of designating size and shape to home ranges for mammals has received considerable attention (Burt 1943; Janes 1959; Brown 1962; Sanderson 1966; and others). For purposes of comparison, home range sizes for wolves in Wood Buffalo National Park were in part determined by the polygon-perimeter method. Area calculations at five-point intervals were similar to those described by Carbyn (1980), except that locations in our case were also expressed over the periods of time during which they

Table 12. Winter home range size of eight instrumented wolf packs on primary bison ranges of Wood Buffalo National Park, 1977-78 to 1980-81, as determined by polygon perimeter method.

Pack	Instrumented wolves	Year	Number of locations	Winter home range size (km^2)
Lake Claire	U270, U271, U273	1977-78	21	1040
Welstead Lake	U268	1977-78	8	265
Hornaday River	U215	1977-78	7	135
Salt Plains	U259	1977-78	6	90
Lake Claire	270, 272, 276, 278, 280, 281-2 285-6	1978-79	14	300
Hornaday River	269, 271, 279, 283-4	1978-79	50	802
Hornaday River	346-7, 348-9	1979-80	101	2393
Hornaday River	346-7, 348-9	1980-81	84	860

Table 13. Comparison of wolf densities in Wood Buffalo National Park[1] with recent studies in other areas of North America, based on radiotelemetry information.

Locality	Southern N.W.T northern Alberta	Northern Alberta	Southern Alaska	Central Alaska	Northern Minnesota		Central Manitoba
Authors	Present study	Fuller and Keith (1980)	Peterson (1980)	Ballard *et al.* (1981)	Van Ballenberghe *et al.* (1975)	Fritts and Mech (1981)	Carbyn (1981)
Major prey	Bison/moose	Moose	Moose	Moose/caribou	Deer/moose	Deer/moose	Elk/moose
Mean annual home range size (km^2)	828	788	585	1390	175	344	260
Winter densities (km^2/wolf)	40-65	158	60-120	97-315	27	56	25-57
(wolves/100 km^2)	1.5-2.5	0.6	0.8-1.7	0.3-1.0	3.7	0.9-3.0	1.8-4.0

[1]Primary winter bison ranges.

occurred. This was considered particularly important as the locational distribution of wolves might not be consistent year-round. Using these criteria, annual home range sizes for 22 instrumented wolves were determined from locations gathered throughout the year, and varied from 220 to 2730 km^2, and averaged 795 km^2 (Table 14). Unlike home range calculations for wolves in Riding Mountain National Park (Carbyn 1980), asymptotes were not readily apparent at any time of the year (Figs. 15-17) and likely reflected seasonal changes in home range size (see below). Ballard et al. (1981), and Carbyn (1980) noted a similar continual increase in home range size for wolves and concluded that although packs occupied the same general area from year to year, their use of outlying areas changed by season and year.

Winter home range sizes were similarly determined for eight packs on primary bison ranges of the park from 1977-78 to 1980-81 (Table 12). Mean home range size during this time was 728 km^2. Home range size for packs could not be determined in summer because packs during this time were commonly split into subunits (Table 15), and instrumented wolves were often not spotted.

Calculations of home range size for wolves in the Hornaday River pack from 1978-79 to 1980-81 using the polygon-perimeter, modified minimum area, mean activity-radius, and atypical habitat-elimination method showed considerable variation (Table 15). The polygon-perimeter method in all cases yielded the largest estimate, followed by the atypical habitat elimination method (since it was based on the former), the modified minimum-area method, and the mean activity-radius method. Within the limitations of circular home range boundaries (Sanderson 1966) the latter

Table 14. Annual home range size of 22 instrumented wolves on primary bison ranges of Wood Buffalo National Park, as determined by polygon perimeter method.

Locality	Wolf number	Year	Number of locations	Home range size (km^2)
Peace-Athabasca delta	U268	1977-78	8	707.4
	U270	1977-78	16	1026.0
	U271	1977-78	20	379.1
	270	1978-79	14	395.5
	272	1978-79	16	219.2
	276	1978-79	15	240.3
	278	1978-79	19	476.5
	281-2	1978-79	19	350.2
	285-6	1978-79	22	406.5
Hay Camp-Darough Creek prairies	U215	1977-78	15	714.6
	U262	1977-78	11	190.8
	269	1978-79	61	1101.7
	271	1978-79	63	942.2
	279	1978-79	49	793.7
	283-4	1978-79	25	1234.7
	346-7	1979-80	105	2142.8
	348-9	1979-80	105	2731.1
	346-7	1980-81	79	754.6
	348-9	1980-81	85	841.7
Salt Plains	U259	1977-78	17	439.6
	323	1979-80	52	544.9
	323	1980-81	23	895.7

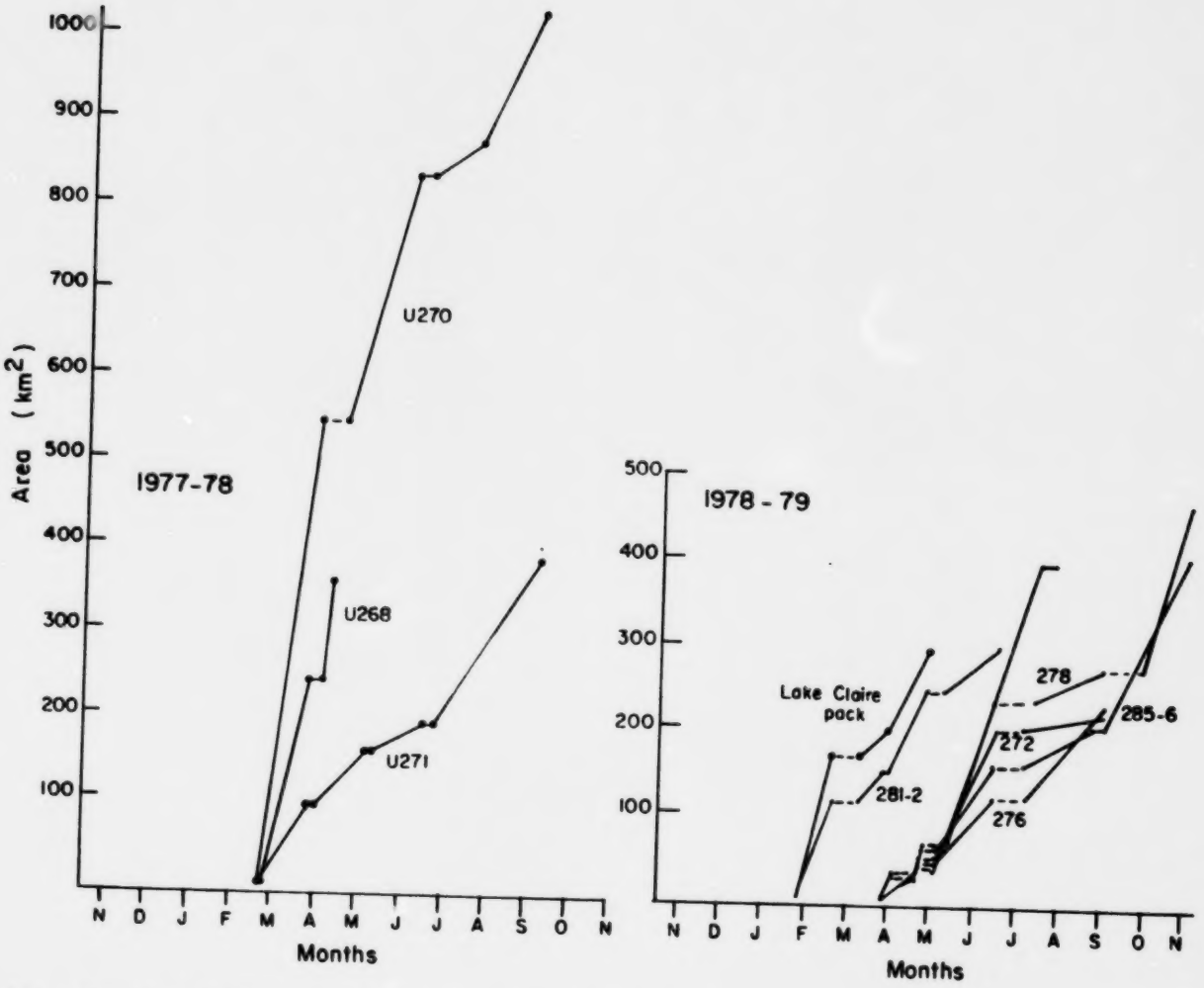


Figure 15. Cumulative home-range size of instrumented wolves in the Lake Claire pack, as determined by 5-interval locations, Wood Buffalo National Park; 1977-78 to 1980-81.

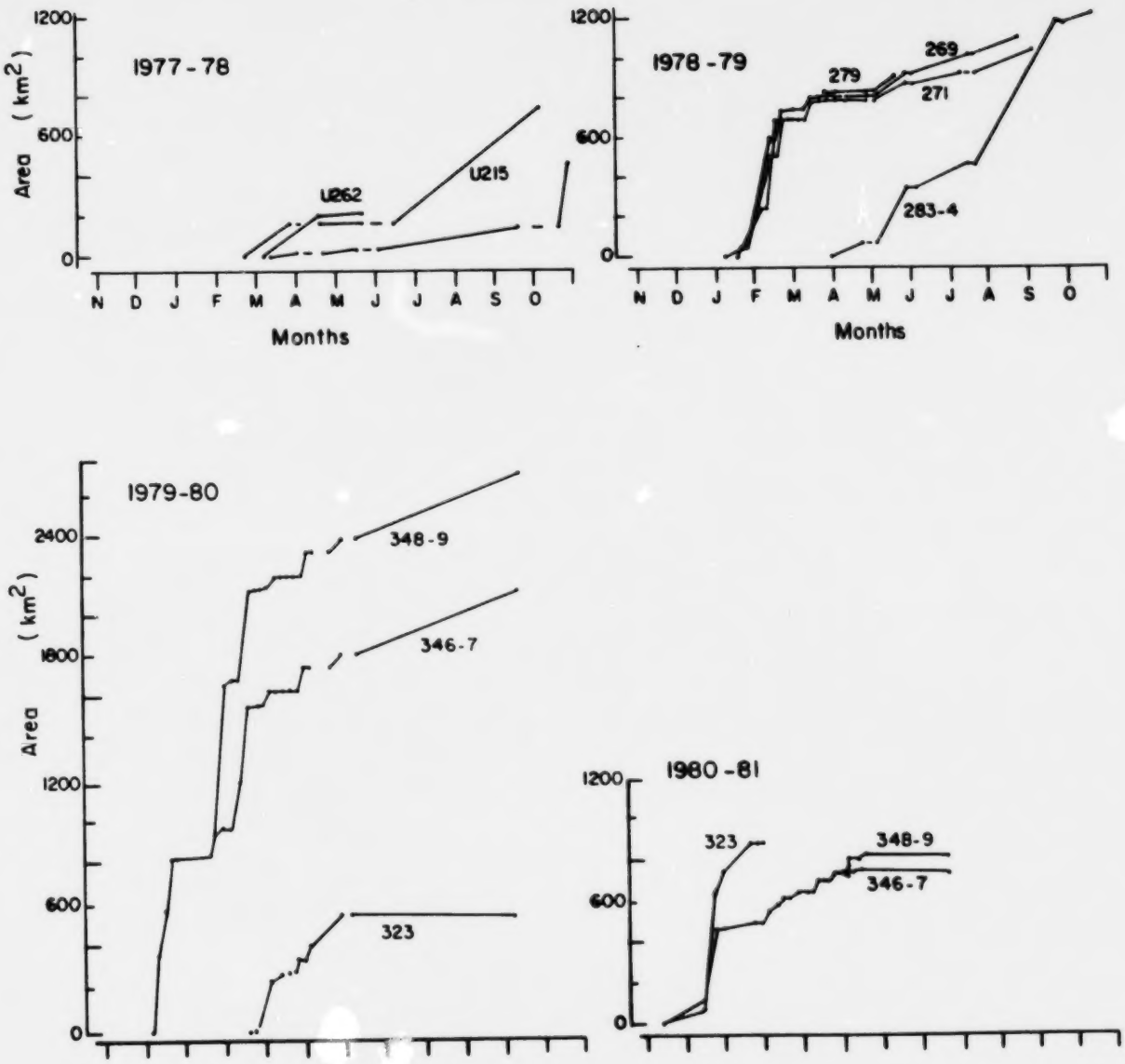


Figure 16. Cumulative home range size of instrumented wolves in the Hornaday River pack, as determined by 5-interval locations, Wood Buffalo National Park; 1977-78 to 1980-81.

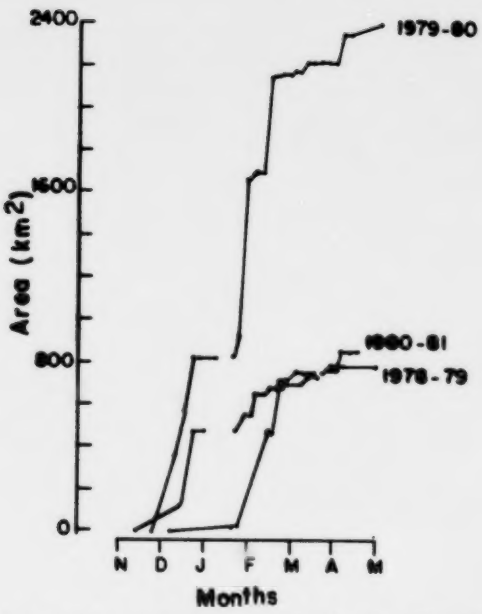


Figure 17a. Cumulative home range size of the Hornaday River pack, as determined by 5-interval locations, Wood Buffalo National Park; 1978-79 to 1980-81.

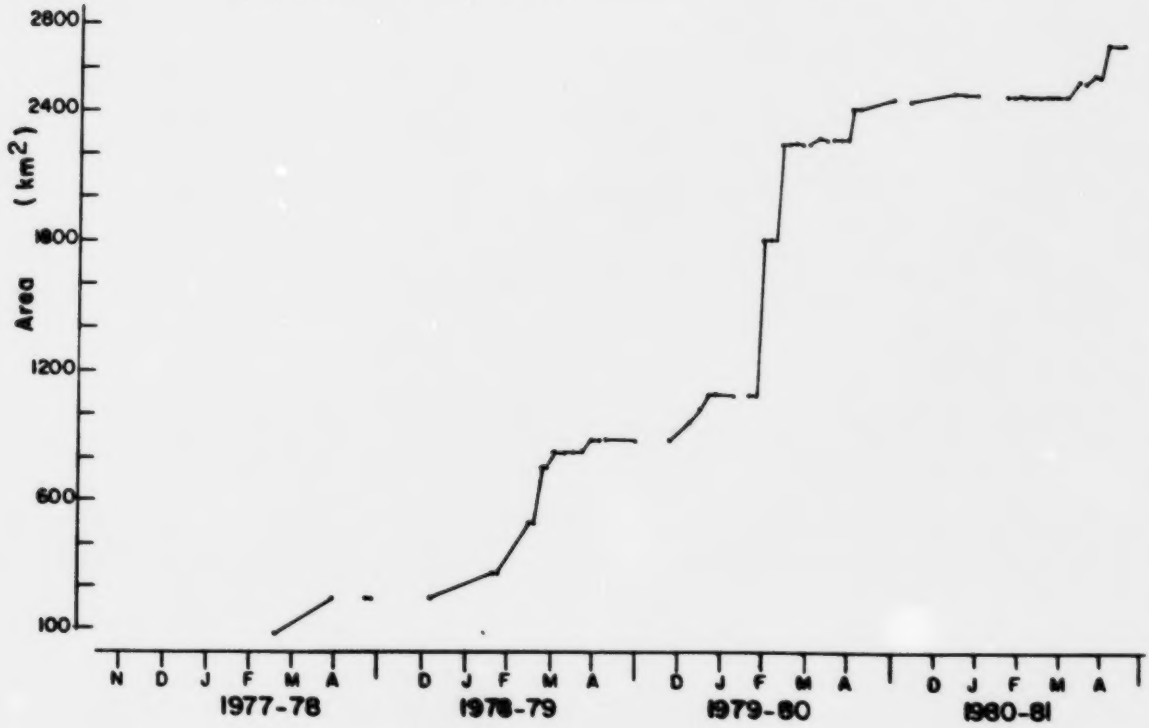


Figure 17b. Cumulative home range of the Hornaday River pack, as determined by 5-interval locations, Wood Buffalo National Park; winters 1977-78 to 1980-81 combined.

Table 15. Home range size of instrumented wolves in the Hornaday River pack, Wood Buffalo National Park, 1978-1981.

Wolf number	Year	Winter home range size (km^2)				Summer home range size (km^2)[5]			
		Polygon perimeter[1]	Modified minimum area[2]	Mean activity radius[3]	Atypical habitat elimination[4]	Polygon perimeter	Modified minimum area	Mean activity radius	Atypical habitat elimination[6]
269	1978-79	807.8	481.4	289.4	665.2	562.6		572.3	
271	1978-79	703.1	336.6	221.6	627.0	597.1		506.6	
279	1978-79	724.2	336.6	254.3	627.0	89.6		346.2	
283-4	1978-79	92.5		171.9	92.5	1174.0	193.1	669.3	
Pack total	1978-79	802.0	558.9	307.8	726.0				
346-7	1979-80	1804.9	1096.1	764.2	1331.4			555.4	
348-9	1979-80	2393.2	1539.9	1231.0	1561.2			939.8	
Pack total	1979-80	2393.4	1539.9	1256.0	1561.4				
346-7	1980-81	754.6	596.2	359.5	754.6				
348-9	1980-81	841.7	639.9	400.9	841.7				
Pack total	1980-81	859.8	639.9	400.9	841.7				
Composite Pack total	1978-81	2739.4	1782.6	648.1	1746.6				

[1]After Mohr (1947).
[2]After Harvey and Barbour (1965).
[3]After Dice and Clark (1953) and Tester and Siniff (1965).
[4]After Ables (1969).
[5]Blanks indicate inadequate number of locations to determine home range size.
[6]Atypical habitat not identified for wolves in summer.

method was particularly sensitive to the frequency with which wolves occupied portions of their home range, although it like the other methods, was considered only an approximation of the actual home range. Winter home ranges of the Hornaday River pack, as determined by the various methods are illustrated in Appendix 3.

Unfortunately sample size was often inadequate to compare winter and summer home range size using the conventional polygon-perimeter method. As an alternative, mean activity radii, or the mean distance between all location points and the geometric activity centre (geometricumean of all location points) were used to compare winter and summer home range sizes of individual wolves (Tables 16, 17).

Examination of these data showed that home ranges of wolves were larger in winter than in summer in the Peace-Athabasca delta (Lake Claire pack), and were generally smaller in winter than in summer in the Hay Camp-Darough Creek prairies (Hornaday River pack). An exception occurred in 1979-80, when the winter mean activity radius of wolf 348-9, and the Hornaday River pack was approximately three times that of pack members in other winters (Table 17), a result of exploratory movements in January and February into the upper Slave River lowlands and the Peace-Athabasca delta.

A comparison of home range sizes north and south of the Peace River showed that using the polygon-perimeter method, mean winter home range size of wolves in Area I was significantly larger ($p < 0.05$) than that in the Peace-Athabasca delta, but was somewhat smaller than that calculated by means of mean activity radii (Table 16). These differences were primarily due to the configuration of winter home ranges in the Peace-Athabasca delta

Table 16. Geometric mean centre of activity and mean activity radius for 22 instrumented wolves on the primary bison ranges of Wood Buffalo National Park; 1977 to 1981.

Wolf number	Year	Winter GMCA	Number of locations	Mean activity radius (km)	Summer GMCA	Number of locations	Mean activity radius	Winter to summer shift in GMCA (km)
U268	1977-78	4360E;64600N	8	14.9				
U270	1977-78	4245E;65315N	7	20.1	4125E;65490N	9	2.9	NNW - 20.0
U271	1977-78	4285E;65160N	9	8.4	4275E;65270N	11	8.4	NNW - 11.0
U215	1977-78	4575E;65970N	7	7.5	4490E;66070N	8	17.0	NW - 13.4
U259	1977-78	4285E;66475N	6	4.6	4225E;66435N	11	9.3	SW - 7.4
270	1978-79	4260E;65190N	7	10.5	4300E;65260N	7	9.0	NNE - 8.0
272	1978-79	4265E;65195N	6	10.8	4270E;65265N	10	5.8	N - 7.3
276	1978-79	4275E;65200N	5	11.5	4290E;65260N	11	6.4	NNE - 7.0
278	1978-79	4275E;65200N	5	11.5	4330E;65260N	14	7.6	NE - 9.0
281-2	1978-79	4230E;65195N	14	11.3	4315E;65260N	5	7.1	NE - 11.3
285-6	1978-79	4260E;65190N	7	10.5	4310E;65240N	15	7.2	NE - 7.3
269	1978-79	4575E;65940N	49	9.6	4495E;66005N	12	13.5	NW - 11.0
271	1978-79	4580E;65930N	49	8.4	4500E;66010N	13	12.7	NW - 12.0
275	1978-79	4555E;65940N	7	3.1				
279	1978-79	4580E;65950N	46	9.0	4505E;65845N	4	10.5	SW - 13.0
283-4	1978-79	4570E;65925N	6	7.4	4540E;65985N	19	14.6	NW - 7.7
346-7	1979-80	4620E;65890N	103	15.6	4445E;66105N	2	17.0	NNW - 28.0
348-9	1979-80	4620E;65850N	103	19.8	4435E;66130N	2	17.3	NNW - 33.3
323	1979-80	4560E;66195N	50	12.5	4585E;66300N	2	13.9	NNE - 11.0
346-7	1980-81	4505E;65990N	78	10.7				
348-9	1980-81	4505E;65995N	84	11.3				
323	1980-81	4605E;66115N	22	18.1				

Table 17. Size of winter and summer home ranges of 21 instrumented wolves on primary bison ranges, Wood Buffalo National Park, as determined by polygon perimeter method (Mohr 1947) and mean activity radius (Tester and Siniff 1965).

Locality	Wolf number	Year	Number of locations		Home range size (km^2)			
					Polygon perimeter		Mean activity radius	
			Winter	Summer	Winter	Summer	Winter	Summer
Peace-Athabasca delta	U270	1977-78	7	9	789.2	41.8	1268.6	26.4
	U271	1977-78	9	11	149.5	88.1	221.6	221.6
	U268	1977-78	7		707.4		697.1	
	270	1978-79	7	7	68.6	183.3	346.2	254.3
	272	1978-79	6	10	50.2	79.2	366.2	105.6
	276	1978-79	5	10	43.6	120.1	415.3	128.6
	278	1978-79	5	14	35.2	242.9	415.3	181.4
	281-2	1978-79	10	9	294.1	86.8	400.9	158.3
	285-6	1978-79	7	15	68.6	215.5	346.2	162.8
Hay Camp-Darough Creek prairies	U215	1977-78	7	8	144.6	240.2	176.6	907.5
	269	1978-79	49	12	807.8	544.5	289.4	572.3
	271	1978-79	49	13	703.1	577.9	221.6	506.5
	279	1978-79	45	4	724.2	84.5	254.3	346.2
	283-4	1978-79	5	20	92.5	1136.3	171.9	669.3
	346-7	1979-80	103	2	1804.9		764.2	555.4
	348-9	1979-80	103	2	2393.2		1231.0	939.8
	346-7	1980-81	78	1	754.6		359.5	
	348-9	1980-81	84	1	859.8		400.9	
Salt Plains	U259	1977-78	6	11	90.0	343.0	66.4	271.6
	323	1979-80	50	2	544.9		490.6	606.7
	323	1980-81	23		895.7			

in 1978-79 (Fig. 18), as drawn by joining a small number of perimeter points (Table 17). Summer home range sizes in both cases were considerably larger in Area I than in the Peace-Athabasca delta, and may have been a result of the year-round availability of bison in the latter area (Oosenbrug et al. 1980a:44).

Dispersal by pack members into summer ranges was measured by geographical shifts in geometric mean activity centres (Figs. 18, 19; Table 16). Mean distance between winter and summer geometric activity centres was 12.8 km; distances by Lake Claire pack members were somewhat less (10.2 km) than those of the Hornaday River pack (16.9 km), and in both localities wolves appeared to respond to seasonal shifts in food resources.

Same-day distances between instrumented wolves were used to express the extent of separation between pack members in summer. Mean same-day distances over the entire summer 1979 were 7.9 km for the Lake Claire pack, and 14.5 km for the Hornaday River pack (Table 18). Circles bounding all locations of instrumented wolves on each day wolves were surveyed in summer are shown in Figure 20 and indicated that pack members in summer were separated by as much as 35 km on any one day.

Pack member separation was temporary, and although packs were most often split into subunits (Table 19), instrumented wolves remained associated throughout the summer. With the exception of female 270, all instrumented wolves in the Lake Claire pack were located at least once with another collared pack member during the summer. Similarly members of the Hornaday River pack maintained an undetermined amount of contact during the summer, and the apparent greater degree of separation between instrumented

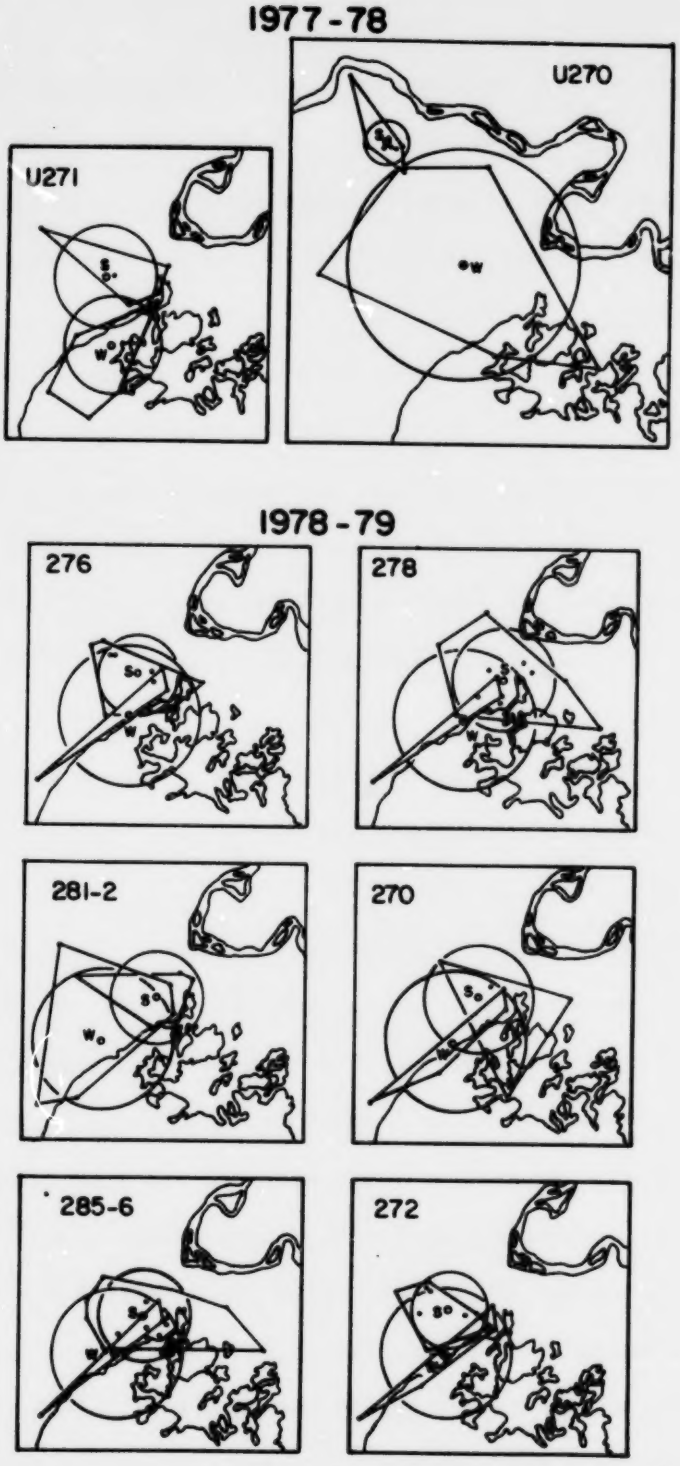


Figure 18. Winter and summer home ranges of wolves in the Lake Claire pack, 1977-78 and 1978-79, as determined by polygon-perimeter method and circles of the mean activity radius.

W = Winter geometric activity centre
S = Summer geometric activity centre

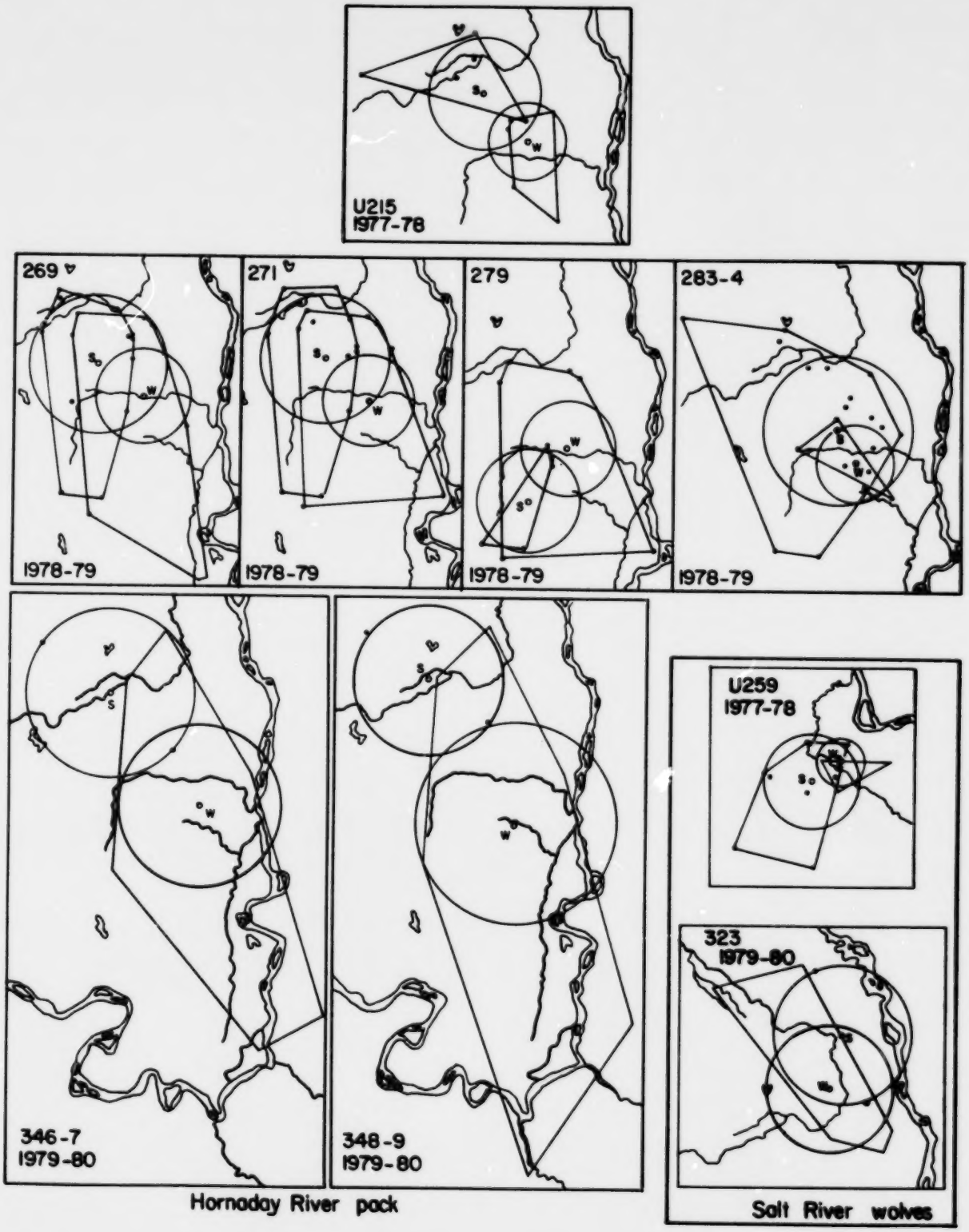
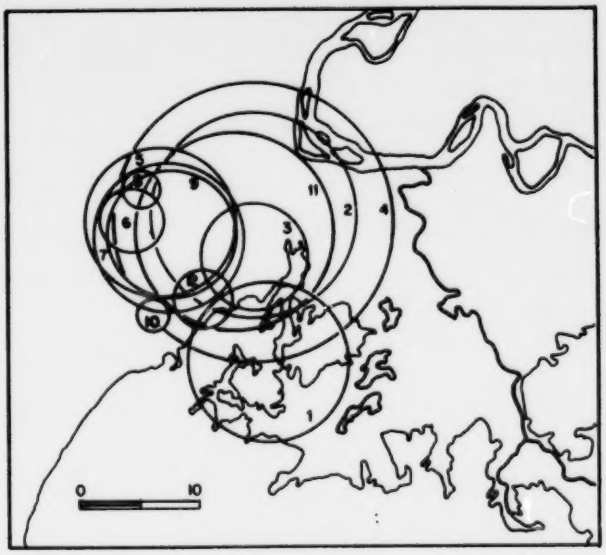


Figure 19. Winter and summer home ranges of wolves in the Hornaday River and Salt River packs, 1977-78 to 1979-80; as determined by polygon-perimeter and circles of the mean activity radius.

Table 18. Mean same-day distance between pack sub-units of the Lake Claire and Hornaday River packs, Wood Buffalo National Park, summer 1979; as determined by radio-tracking of instrumented wolves.

Date	Lake Claire pack				Hornaday River pack			
	Map reference number	Number of instrumented wolves	Number of pack sub-units	Distance (km)	Map reference number	Number of instrumented wolves	Number of pack sub-units	Distance (km)
06/05/79	1	6	3	8.3				
16/05/79	2	5	4	8.8	1	4	3	3.1
22/05/79	3	6	3	5.7	2	4	3	10.5
30/05/79					3	3	3	14.2
06/06/79	4	6	5	14.1	4	3	3	12.3
09/06/79					5	3	2	16.4
15/06/79	5	6	2	12.1	6	2	2	1.1
25/06/79					7	2	2	13.1
10/07/79	6	3	3	9.7	8	3	3	19.5
16/07/79	7	5	3	8.1	9	2	2	23.8
21/07/79	8	5	3	2.2	10	3	2	34.8
26/07/79	9	4	4	7.7				
25/08/79	10	4	2	2.4	11	3	2	21.3
05/09/79	11	4	4	11.7	12	2	2	4.5
17/10/79	12	2	2	4.3				
Mean				7.9				14.5



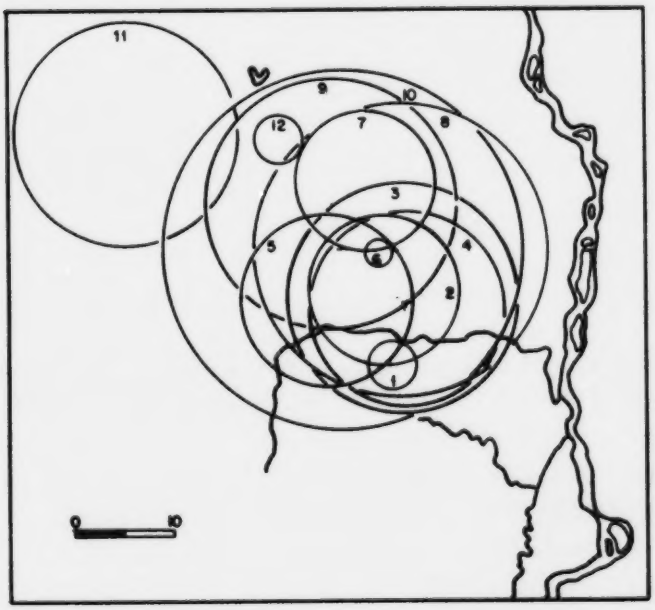


Figure 20. Circles bounding same-day maximum distances between members of the Lake Claire and Hornaday River packs, summer 1979. (See tables for corresponding dates.)

Table 19. Cohesion and splitting of wolf packs in winter and summer on primary bison ranges, Wood Buffalo National Park; 1977-78 to 1980-81, as determined by occurrences of pack sub-units.

Pack	Year	Number of instrumented wolves	Number of pack sub-units											
			1		2		3		4		5		Total	
			W	S	W	S	W	S	W	S	W	S	W	S
Lake Claire	1977-78	2-3	0	0	5	14	5	0					10	14
	1978-79	2-6	14	3	0	3	0	5	0	3	0	1	14	15
Hornaday River	1977-78	2	3	0	2	0							5	
	1978-79	2-4	41	2	7	7	3	5					51	14
	1979-80	2	95	1	8	1							103	2
	1980-81	2	73	1	9								82	1

W = Winter, S = Summer

Table 20. Utilization of home range area by the Hornaday River pack, as determined by number of locations per 6.25 km^2 unit.

Year	Number of 6.25 km^2 units in home range	Locations per square unit									
		1	2	3	4	5	6	7	8	9	10
1978-79	39	25	7	5	1	1					
1978-79	69	47	14	3	4	1					
1980-81	48	26	12	4	5	1					
1978-1981	107	54	21	7	9	5	4	5	1		1

Table 21. Theoretical and actual number of locations of the Hornaday River pack[1] within the mean activity radius in winters 1978-79 to 1980-81.

Year	Geometric mean activity centre	Total number locations	Mean activity radius (km)	Number of locations	
				Observed	Expected
1978-79	4580mE; 65950mN	65	9.1	39	44
1979-80	4620mE; 65850mN	103	20.0	72	70
1980-81	4560mE; 65970mN	84	11.3	54	57
Composite 1978-1981	4590mE; 65915mN	252	14.6	165	172

[1]Includes locations of all members.
[2]Expected number of locations based on 68.26% proportion within standard diameter (Dice and Clark 1953).

wolves (Fig. 21) was most likely a result of the lesser number of instrumented individuals.

Since wolves were located irregularly in summer, it was generally not possible to pinpoint geographical centres of activity. However, ground observations in areas of habitual summer use, as determined by aerial radio tracking (Fig. 22) made it possible to locate denning and rendezvous sites.

Adherence, or fidelity of the Hornaday River pack to certain portions of its winter range was determined for each summer 1978-79 to 1980-81, as well as for the three winter periods from 1978 to 1981, since marked wolves were present in the pack for at least that period of time. Frequency histograms (Fig. 23) of 6.25 km^2 units of the home range occupied each year and over the duration of the study indicated that most portions of the home range were used only occasionally during the course of each winter, but some portions were consistently heavily utilized (Figs. 24, 25). Not unexpectedly the latter areas consisted primarily of prairies and meadows (Fig. 26), which also comprised prime winter habitat for bison.

In terms of area allocation for two or more locations per square unit, 60% of locations were recorded in 36% of the area occupied in 1978-79, 51% in 32% in 1979-80, 70% in 46% in 1980-81, and 79% in 50% of the area in winters 1978-79 to 1980-81 combined. Similarly the proportions of locations within the area circumscribed by the mean activity radius, or standard diameter (Fig. 27, Table 20) closely resembled the theoretical 68.36% of all locations in each winter (Dice and Clark 1953) and thus was considered an adequate definition of the area of concentrated use.

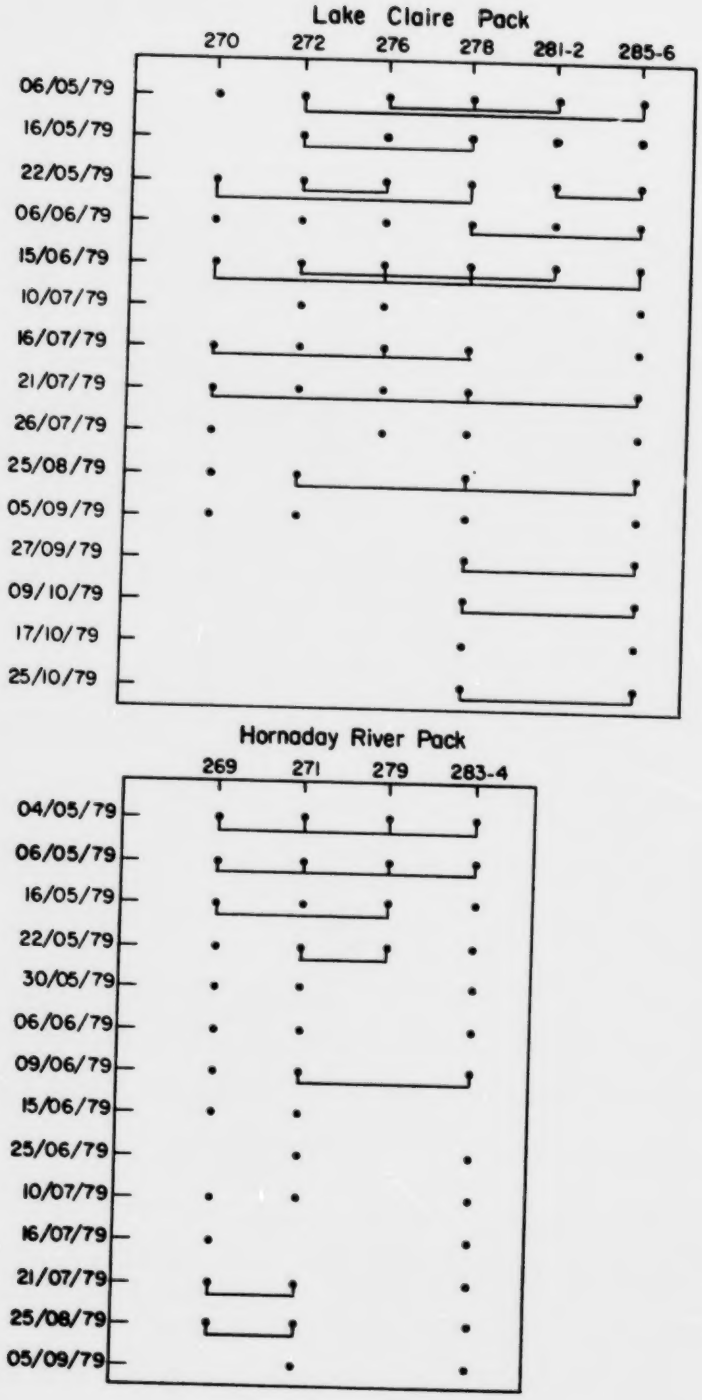


Figure 21. Association between pack members of the Lake Claire and Hornaday River pack, summer 1979; Wood Buffalo National Park.

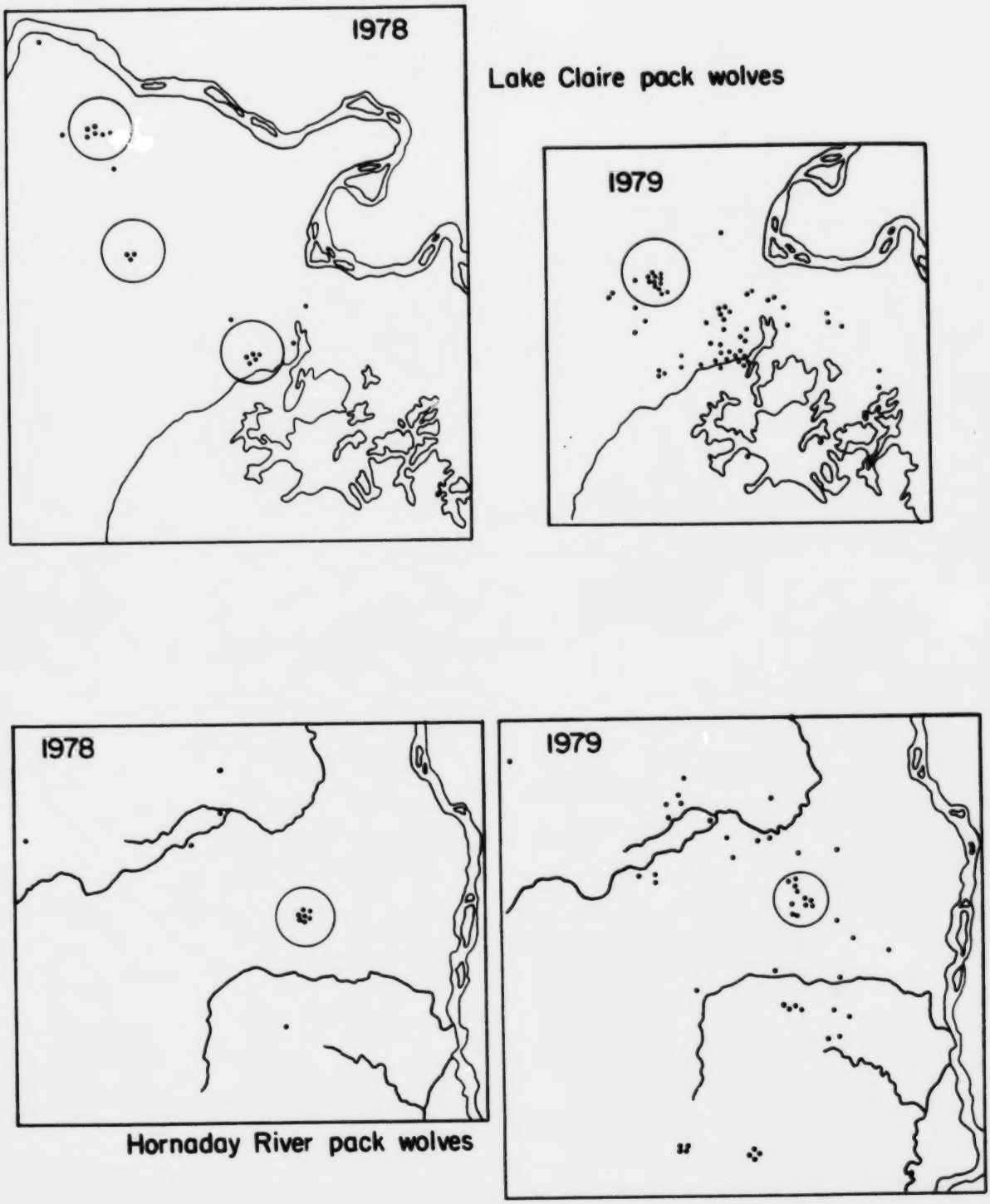


Figure 22. Geographical distribution of location points for the Lake Claire and Hornaday River pack wolves, summers 1978 and 1979, showing areas of concentrated activity.

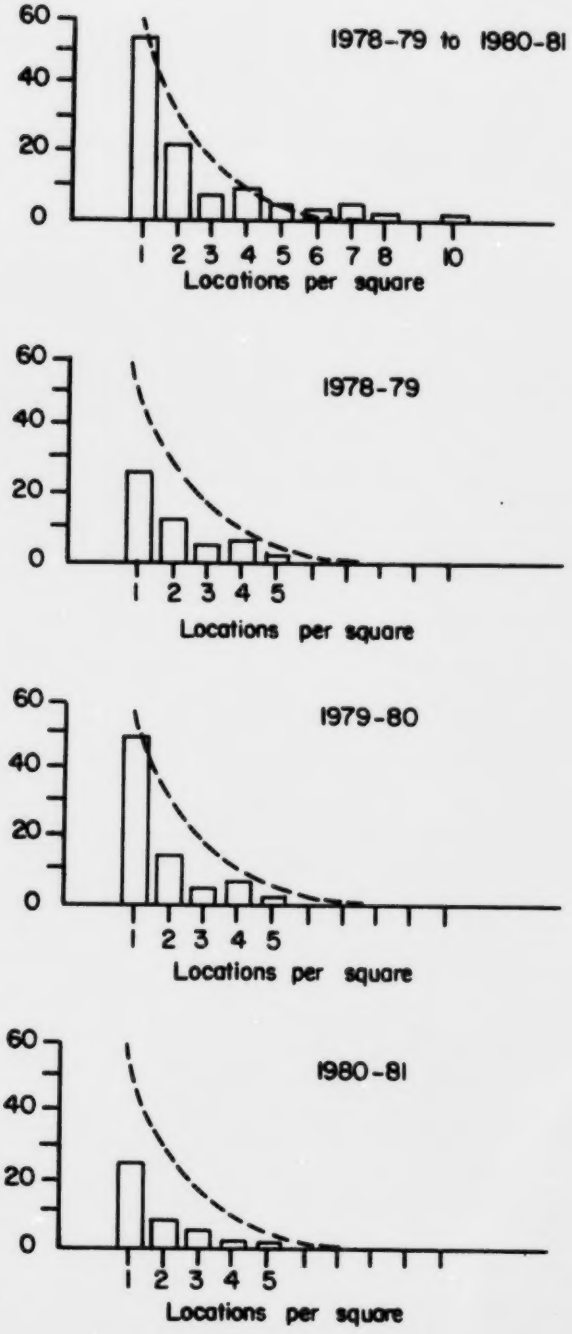


Figure 23. Frequency distribution of number of locations per 6.25 km^2 units in the home range of the Hornaday River pack occupied in winters 1978-79 to 1980-81, Wood Buffalo National Park.

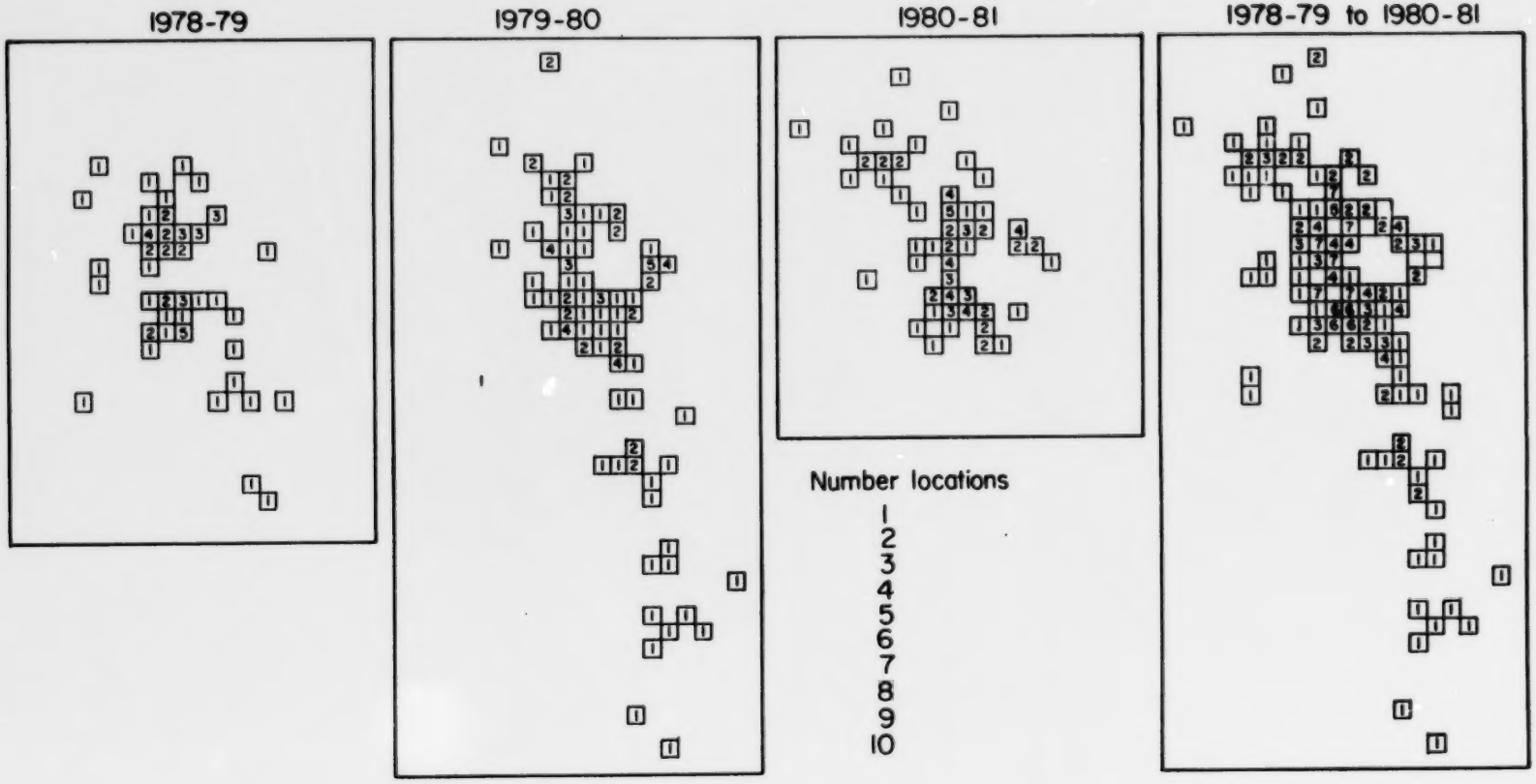


Figure 24. Utilization of winter home-ranges of the Hornaday River pack, as determined from number of locations in 6.25 km^2 units; 1978-79 to 1980-81.

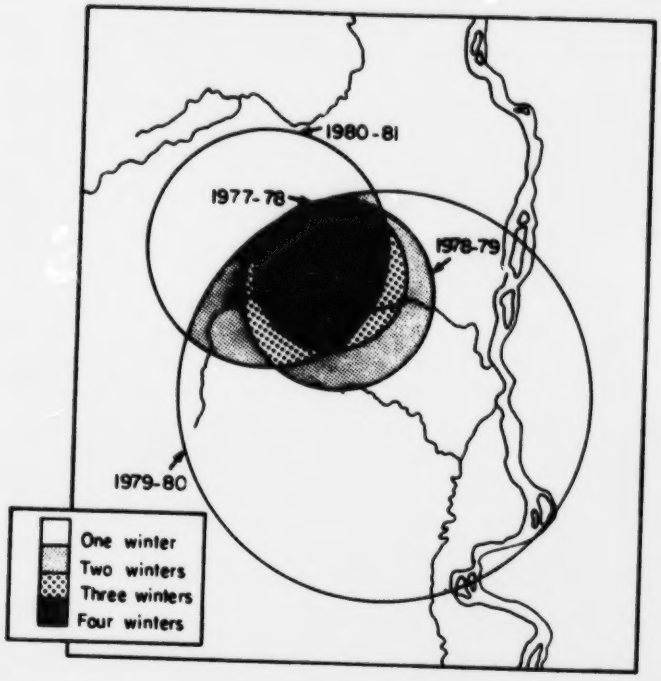


Figure 25. Overlap in mean activity radii for the Hornaday River Pack, winters 1977-78 to 1980-81; Wood Buffalo National Park.

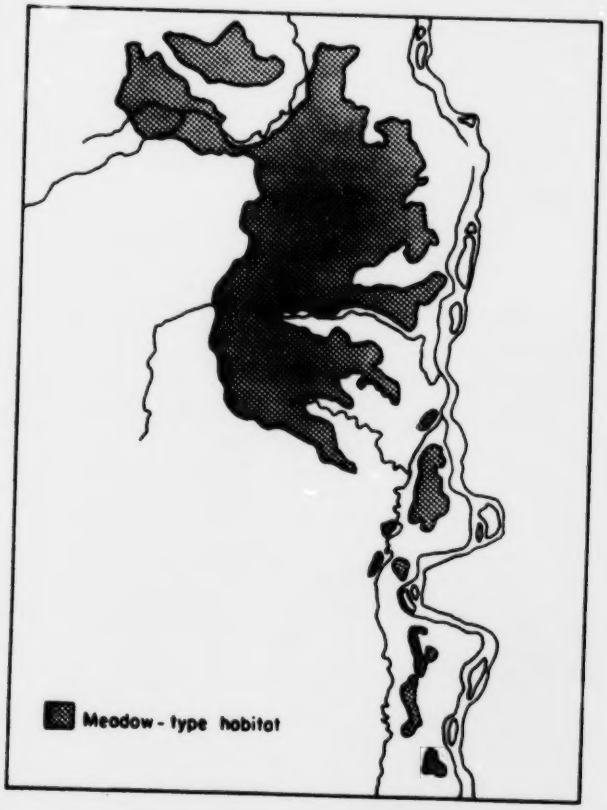


Figure 26. Location of areas of meadow-type habitat within the home range of the Hornaday River pack; Wood Buffalo National Park.

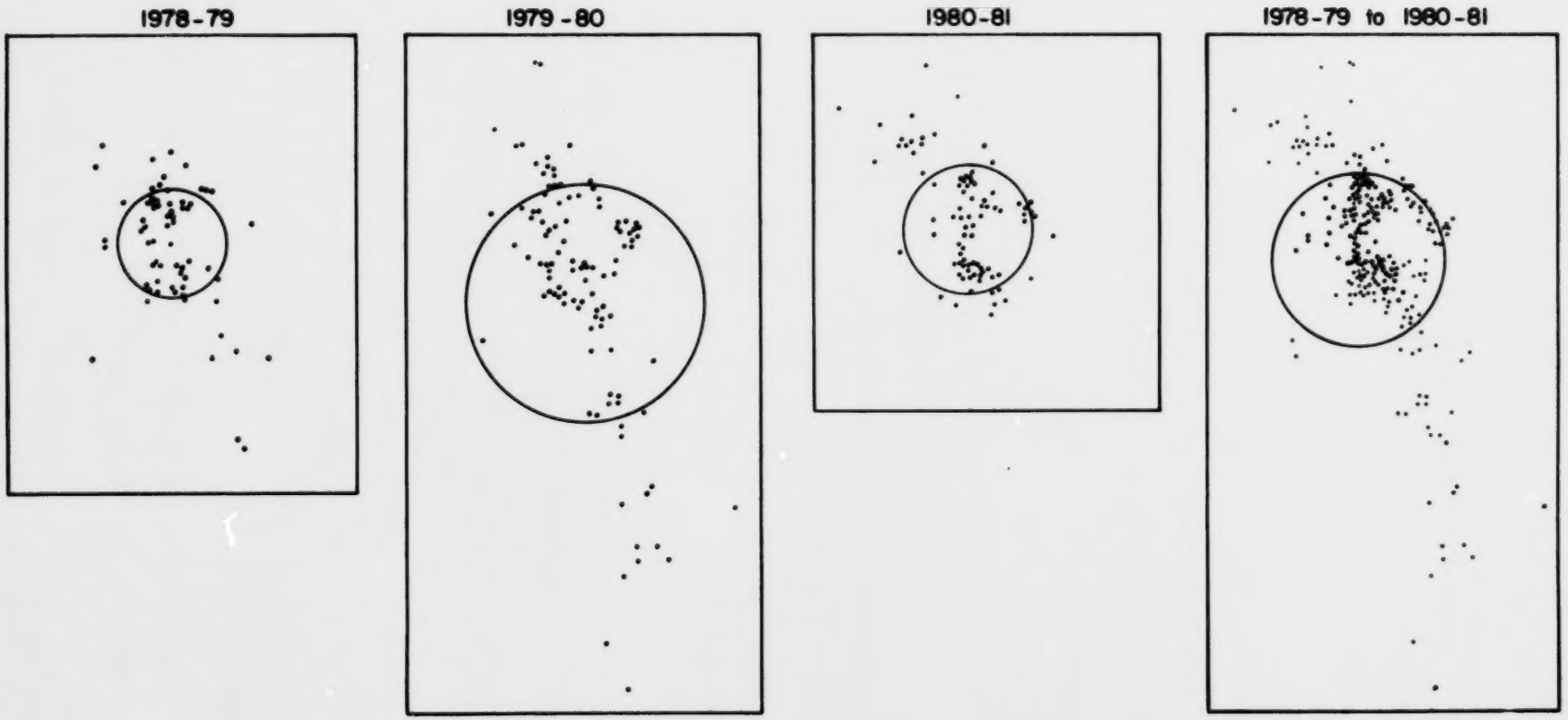


Figure 27. Distribution of location points and circles of mean activity radii of the Hornaday River pack, 1978-79 to 1980-81; Wood Buffalo National Park.

Comparisons of our home range data with those of other studies could be made only for size calculations based on the conventional polygon-perimeter method. On this basis annual home range sizes for packs in winter in Wood Buffalo National Park were considerably larger than those reported for wolves preying on deer (Odocoileus virginianus) in Minnesota and Ontario (Mech and Frenzel 1971; Kolenosky 1972; Van Ballenberghe et al. 1975; Fritts and Mech 1981), for wolves and moose in Isle Royale (Peterson 1977), and wolves and elk (Cervus canadensis) in Manitoba (Carbyn 1980).

Fritts and Mech (1981) calculated the composite annual home range of eight packs over several consecutive years and found that ranges varied from 195 to 555 km^2. They reported no geographical shifts from winter to summer and packs apparently remained cohesive in summer. The composite home range of the Hornaday River pack was 2740 km^2 during winters 1977-78 to 1980-81. The dispersal of pack members into separate, although probably temporary subunits made it difficult to define the pack's summer range, but inclusion of location points for all instrumented wolves in summer increased the size of the year-round home range to over 3000 km^2.

Our data on home range size in relation to five-point interval locations suggested that in 1979 the winter home range for the Lake Claire pack was probably not adequately defined due to a small number of locations. Summer locations indicated differences in home range size between pack members, both in 1978 and 1979, although it was not possible to follow into the next winter any possibly dispersing wolves such as male U270 (Fig. 15).

Home range size appeared to be adequately defined for the Hornaday River pack at approximately 800 km^2 in 1978-79, 1979-80, and 1980-81

(Fig. 17a), but dispersal of wolves in summer, as well as an apparent range expansion in 1979-80 (Fig. 17b) resulted in a much larger total area. The latter event appeared to have been a temporary incursion into areas occupied by adjacent wolf packs, since the Hornaday River pack primarily occupied its pre-1980 home range again in 1980-81 (Fig. 28). However, rapid changes in home range size were interpreted as shifts by packs into adjacent "territories" (Carbyn 1980), and this may also have been the case for the Hornaday River pack in 1980, since pack size for the instrumented unit decreased from 14 to seven between April and November 1980 (see earlier discussion) possibly as a result of a permanent split in the pack.

Summer home ranges of wolves varied in size from 41.8 to 1136.3 km^2 (Table 17), although the number of locations in some instances was very small. Geographical shifts from winter to summer home ranges were evident in all cases, but have not generally been documented for wolves in other areas (Carbyn 1975, Van Ballenberghe et al. 1975; Fuller and Keith 1980; Fritts and Mech 1981). These shifts appeared to be a result of bison movements northwest away from Lake Claire, and northwest out of the Hay Camp-Darough Creek prairies into the Alberta Plateau, and may be similar to observations of wolves moving northward with caribou herds which are travelling from winter to summer areas (Heard, pers. comm.)

Differences in summer home range size between members of the Lake Claire and Hornaday River packs may have been a reflection of the relative distance that bison move in each of these localities from winter to summer ranges. Home range sizes for the Hornaday River pack wolves in summer were considerably larger than those of the Lake Claire pack, however, mean distances between consecutive locations were not (Table 22), suggesting

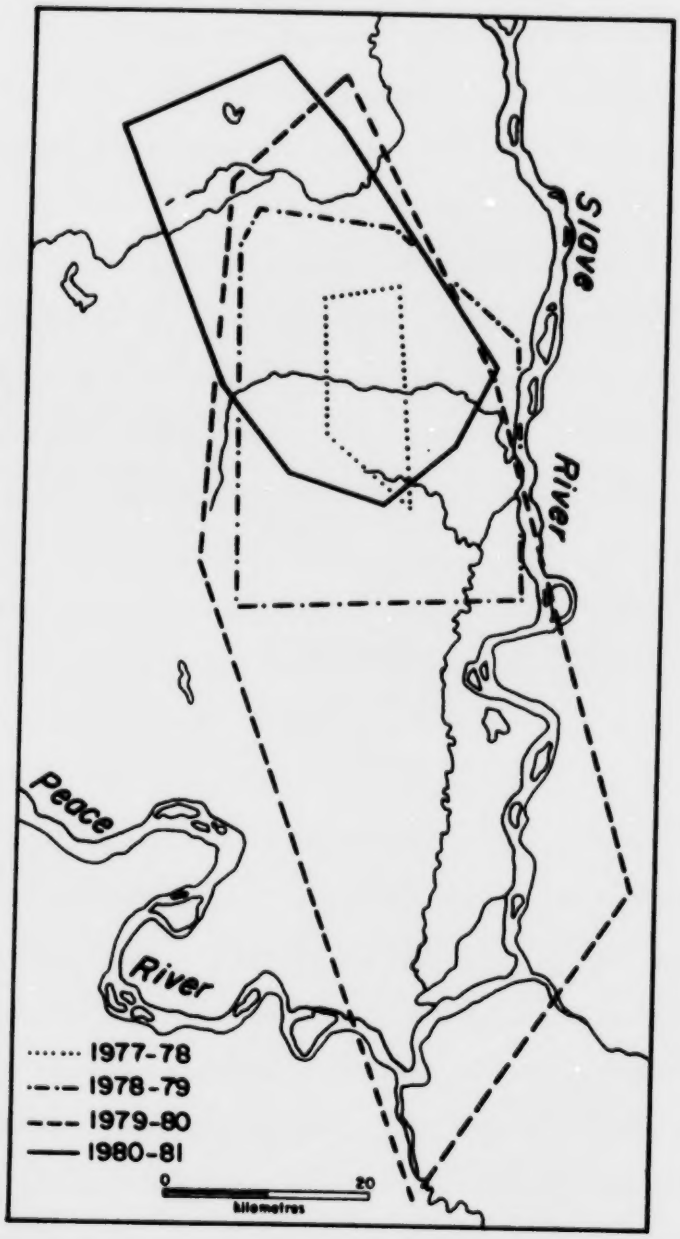


Figure 28. Winter home ranges of the Hornaday River pack, 1977-78 to 1980-81, Wood Buffalo National Park; as determined by the polygon-perimeter method (Mohr 1947).

Table 22. Mean straight-line distances between locations of instrumented wolves in the Lake Claire and Hornaday River packs, Wood Buffalo National Park; summer 1979. (Number of locations are in brackets.)

Pack	Wolf number	Mean number days between locations	Mean distance (km) between locations
Lake Claire	270	13 (5)	12.7
	272	13 (8)	13.1
	276	12 (9)	15.3
	278	14 (11)	16.9
	281-2	10 (3)	17.9
	285-6	13 (12)	18.2
Mean		12 (48)	15.9
Hornaday River	269	11	17.0
	271	11 (10)	13.1
	279	6 (1)	6.8
	283-4	10 (15)	24.7
Mean		10 (35)	15.4

that wolves in both areas traveled similar distances, but the Hornaday River pack wolves traveled farther afield in response to greater bison movements.

5. Territoriality and intraspecific relations

The theoretical concept of territoriality has been applied to wolves by various authors in Ontario (Kolenosky 1972; Pimlott et al. 1969), Isle Royale (Jordan et al. 1967; Wolfe and Allen 1973), and Minnesota (Mech 1972, 1973; Carbyn 1980). Not until recently have radiotelemetry studies enabled a more precise understanding of the spatial-temporal relationships between wolves.

Burt (1943) defined home ranges as "areas over which an animal normally travels in search of food," whereas territories were considered that part of the home range defended against conspecifics. In some cases (Van Ballenberghe and Erickson 1973; Wolfe and Allen 1973; Mech 1977; Peterson 1977; and Carbyn 1981) defense of living space, i.e. physical contact between packs, has been observed, however, other less overt forms of "territorial behaviour" such as scent marking (Peters and Mech 1975), howling (Harrington and Mech 1979), and avoidance (Peterson 1977) have been more commonly documented.

Van Ballenberghe et al. (1975), Mech (1973, 1977a), and Peters and Mech (1975) implied that wolf packs in northern Minnesota were territorial in their entire home ranges, and that these areas were largely exclusive and non-overlapping. In addition to packs, an unknown number of lone wolves and pairs also circulated within pack territories. Data on Alaskan wolves (Ballard et al. 1981) support these observations, however, studies

on Isle Royale (Peterson 1977) and in Riding Mountain National Park (Carbyn 1980) document considerable overlap in wolf territories. Ballard et al. (1981) reported that pack territories in central Alaska were essentially non-overlapping and defended, although intrusions into neighbouring territories often occurred when the home pack was absent from that portion of the area.

Mech (1977a, b) and Hoskinson and Mech (1976) showed that the degree of overlap in territories tended to increase with reduced food availability whereby wolves in neighbouring packs trespassed in search of prey. Zimen (1976) speculated that territory size was in part governed by prey availability, and Mech (1977a), Peterson (1977) and Haber (1977) agreed that food shortages were primarily responsible for increases of trespassing into neighbouring territories, although Carbyn (1981b) reported evidence of trespass and pack displacement which occurred in the absence of food shortages.

The question of whether territoriality exists in wolf packs preying on clumped and mobile prey species such as caribou and bison has only been partially answered. Burkholder (1959), Kuyt (1972), Parker (1973) and Stephenson (1978) implied that wolves traveled with migrating caribou into areas of winter concentration, although no observations of intraspecific tolerance were noted. Recent radiotelemetry data from wolves captured and instrumented on the winter range of the Beverly caribou herd, Northwest Territories, indicated that in late winter wolves tend to travel hundreds of kilometres with the caribou toward their calving grounds (D. Heard, pers. comm.). Van Camp (1980) documented considerable overlap in the territories of what he assumed were three neighbouring packs that preyed on

approximately 300 bison in the Slave River lowlands in late winter 1976-77.

Home range overlap in our study area (Fig. 29) was documented for two neighbouring instrumented packs during winters 1979-80 and 1980-81, and for two instrumented packs in late summer 1979, (Table 11). On 1 February 1980, a pack of seven unmarked wolves was resting on the bank of the Salt River within the winter home range of the Hornaday River pack and killed a bison a few hours later south of the river. The pack remained in the vicinity of the kill for a week. Three of its members were captured and instrumented, but due to an attack by the Hornaday River pack on 24 February, the group was scattered and two of the instrumented wolves killed. The remaining wolf, (male 323) subsequently returned to the kill and later in March spent 13 consecutive days near another bison carcass at the edge of the Hornaday River pack's range. It apparently reestablished only temporary ties with other surviving pack members, since only on three occasions was it located with other wolves, each time outside the Hornaday River pack's winter range. During this time it was recovering from a trap-inflicted injury to one of its feet, and apparently was unable to travel with the pack.

In 1980-81 a group of three wolves, including 323 and a former member of the Hornaday River pack (283-4?) spent approximately 50% of its time within the boundaries of the Hornaday River pack's winter range (Fig. 29). The former Hornaday River pack wolf was believed to have been a dominant male in 1978-79, and was dominant over wolf 323 and the other wolf of unknown sex. Its previous knowledge of the Hornaday River pack's winter range was evident in the extent these three wolves occupied this area.

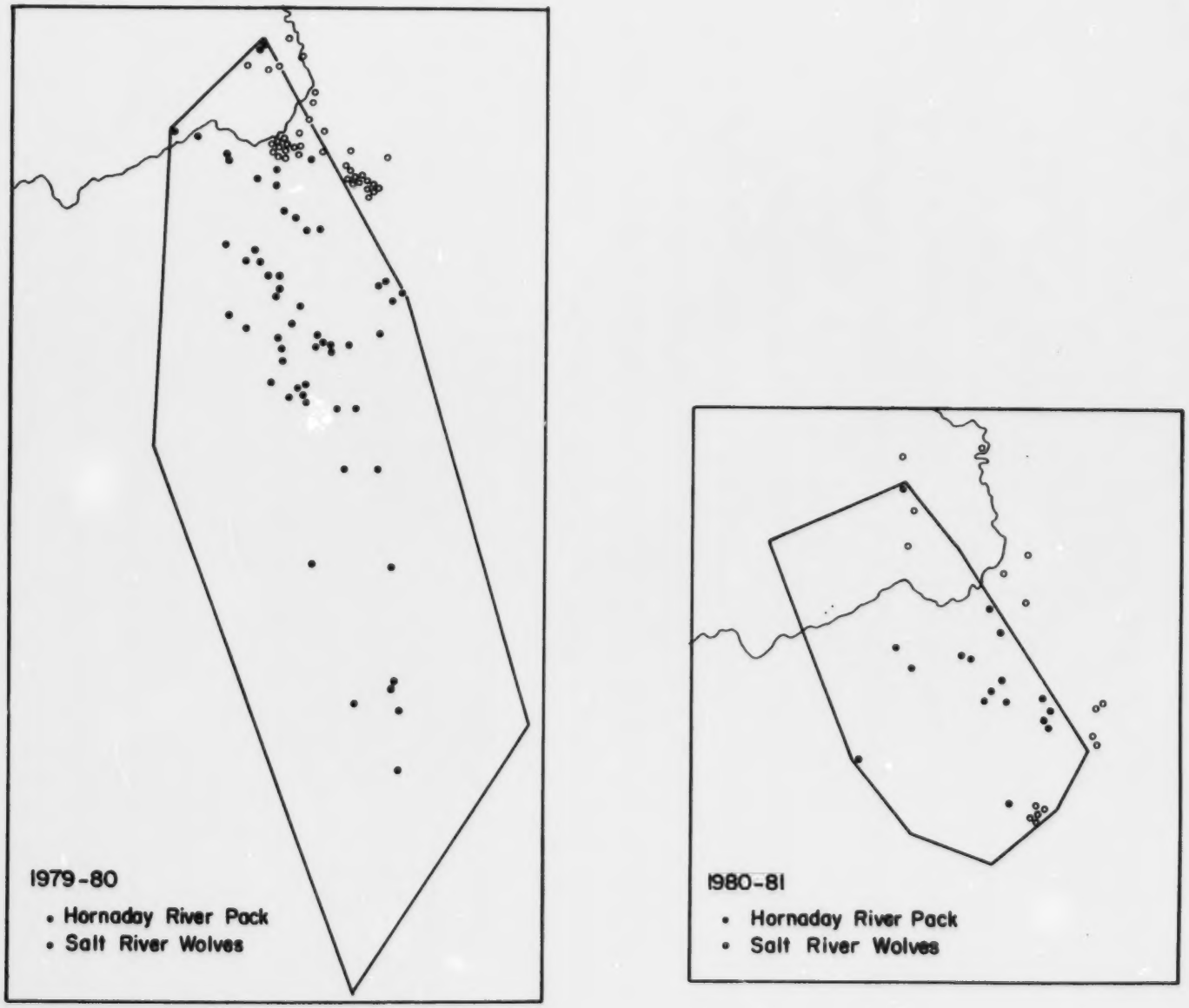


Figure 29. Location of Salt River wolves within and adjacent to the annual winter home range of the Hornaday River pack, Wood Buffalo National Park; 1979-80 and 1980-81.

Association between unrelated wolves has been shown recently to occur in northwestern Minnesota (Fritts and Mech 1981), where in an expanding population, it commonly led to formation of new packs.

In late October 1979 the Lake Claire pack (12 wolves) was located in the area occupied by the Baril Lake pack the previous winter. As the Baril Lake pack was not under surveillance at this time, it is not known whether the area had already been vacated by the pack, the pack was in another part of its range, or the Lake Claire pack had displaced the Baril Lake pack.

In other cases pack affiliation of wolves was not always possible, however, a number of instances where evidence of wolves not normally associated with the Hornaday River pack, were found within the boundaries of the Hornaday River pack's composite home range. These intrusions, or potential overlap of home ranges, may have occurred as a result of annual, seasonal or even shorter term excursions by the Hornaday River pack from portions of its home range.

Fidelity by the Hornaday River pack to certain parts of its home range was evident (Figs. 24, 25). Approximately 65% of all pack locations between 1978-79 and 1980-81 were recorded within the 670 km^2 circle bounding the mean activity radius for those years (Table 21); no packs other than the one of questionable status (Darough Creek pack) were ever located within its boundaries. Movements of the Hornaday River pack more than 25 km away from the periphery of this home range core occurred twice in midwinter 1980, when the pack travelled south into areas known to have contained at least two other packs the previous year. In both instances the pack made a kill. In late March 1980 the pack traveled 18 km north of

its home range core and visited a den site thought to have been occupied by the Salt River pack the previous summer.

An encounter between the Hornaday River pack and the intruding Salt River pack on 24 February 1980 led to the death of at least three members of the latter pack. The Salt River pack killed a male bison and fed on the carcass for almost a week. The kill was outside the home range core but inside the 1979-80 periphery of the Hornaday River pack's winter range. During this time the Hornaday River pack traveled within 3 km of the kill site and the Salt River pack (Fig. 30). Notes on the encounter were as follows: "Left Fort Smith per aircraft at 1035. Trace of snow overnight, mostly sunny, -20°C with winds SE 10-15 kph. Salt River signals separated today. Spent about 40 minutes searching for wolves. At 1100 spotted one dark-grey wolf and what looks like remains of a wolf on Salt river 500 m northeast of bison carcass. Signal of 323 nearby. Signal of 322 at junction of small creek and Salt River - not spotted. Signal of 324 still near bison carcass, then spotted lying on snow 100 m northeast of kill. Fly low over wolf; it looks mauled and lifts head as plane passes over. At 1135 spot Hornaday River pack (12 wolves) moving 100 m south from bison carcass; tracks indicate they have come from the carcass."

"Skidooed into the area in afternoon but deep snow bogged down machine and had to return to camp at 1915. Next day try again, made it to bison carcass and wolf 324. Tracks indicate a chase heading northeast toward the Salt River; apparently wolf 324 (juvenile female) was caught and killed only 100 m from where the chase began. Tracks continue to lead toward the river, although it appears the Hornaday River pack did not pursue the Salt River wolves beyond the carcass of wolf 324."

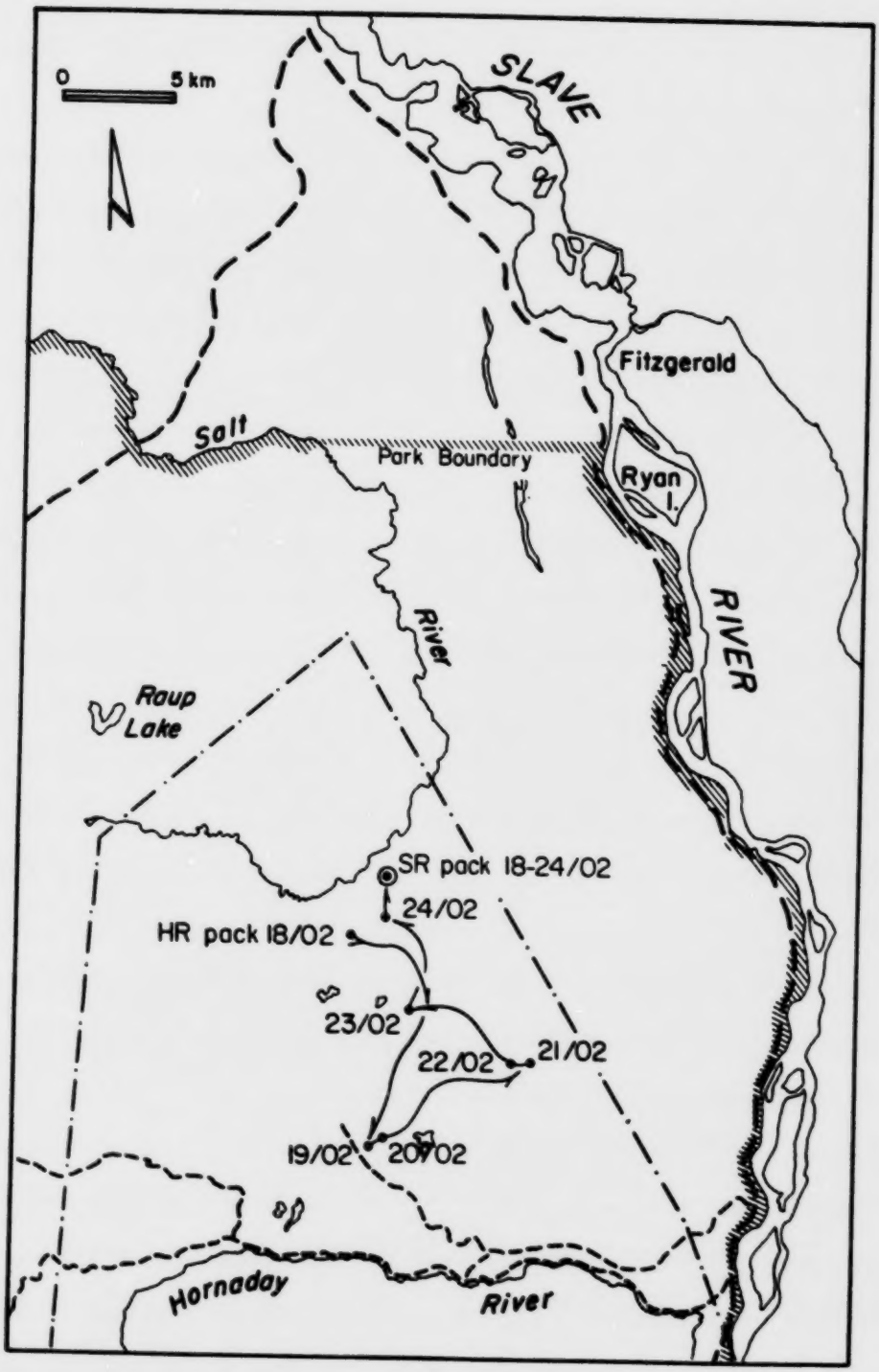


Figure 30. Location of Hornaday River and Salt River packs from 18-24 February, and northern periphery of Hornaday River pack home range, winter 1979-80, Wood Buffalo National Park.

Carcasses of male 322 and an unidentified adult animal (sex unknown due to probable scavenging by members of the Salt River pack) were recovered later. Male 322 discovered intact beneath a large spruce tree, apparently died of puncture wounds to the back and abdomen. The latter carcass was that of the wolf observed on the Salt River on 24 February; its pelvis and hind legs had been removed from the torso, plus the front paws, lower abdomen and part of the neck were missing. Patches of fur and hide were scattered among numerous wolf tracks, although it was evident the carcass had also been fed upon by ravens (Corvus corax). Further evidence of wolves killing other wolves was obtained. In February 1978 a trapper gave us the carcass of a juvenile female wolf which he believed had been killed by other wolves in the area of Sweetgrass Island. This wolf had puncture wounds in the side and dorsal area of the neck, cranium, rib cage and rump, similar to the three wolves killed in 1980.

On 3 April 1980 we recovered the partially consumed carcass of an immature wolf which had died or been killed recently. This carcass was found near the suspected Salt River den site of 1979, which had been visited on 30-31 March 1980 by the Hornaday River pack. Judging by its size and teeth, the carcass was that of a pup not older than eight months, a similar case was reported by Fuller (1953). The Hornaday River pack had evidently fed on the carcass, as there were numerous trails leading from the den to the carcass. Two somewhat circular areas each about three metres across, with the carcass in the centre of one, suggested the wolves had dragged or struggled with the wolf.

In summary, we suspect that the Hornaday River pack, maintained a home range core exclusive of other packs, but frequently ventured into areas outside this core. The reasons for these forays into peripheral areas, and adjacent pack home ranges are poorly understood. Wolves in Wood Buffalo National Park may at least be partially food motivated, as was the case for the Salt River pack in February 1980 (few bison were recorded on surveys north of the Salt River in winter 1979-80). The Hornaday River pack also may have ventured into foreign terrain in response to bison movements, although it is possible circumstances relating to pack instability may have resulted in the unprecedented movements of the Hornaday River pack in 1980.

6. Reproduction and denning ecology

The onset of the breeding season for wolves in Wood Buffalo National Park, as indicated by increased social interactions between pack members, pair bonding, vaginal bleeding (proestrus), and mounting and coupling occurred from 11-16 February during the three winters of observation (1978-79 to 1980-81). Although signs of vaginal bleeding were recorded from 16 February to 16 March (1979), sexual interaction between pack members was most intense between 15-28 February (Table 23). Mounting attempts were recorded on 13 and 16 February 1981. An apparent successful coupling between alpha male and a subordinate female occurred on 16 February.

Timing of mating activity in our study area coincides with observations in Alaska (Haber 1977) from 18 Februry to 18 March, northern Alberta (Fuller and Keith 1980) from 21 February to 6 March, northeastern Minnesota

Table 23. Breeding activity and related behaviour of the Hornaday River pack from onset of reproductive cycle to end of winter, 1979 to 1981. (Den numbers in brackets.)

Date	Event
1979	
February 16	Vaginal bleeding on trail near 1978 den
20	Unrest in pack; posturing and dominance displays by alpha pair
21	Blood spots (vaginal bleeding) in two beds south of Raup Lake
24	Den diggings and tracks near Salt River (1)[1]
March 14	Den diggings in southeast island (2)[2]
16	Den diggings at north end of Hay Camp meadows (3)[2]; two bedding sites vaginal bleeding
1980	
February 18	Vaginal bleeding on bedding site (Salt River pack)
21	Unusual amount of interaction of pack members
March 30-1	Pack at freshly dug den near Salt River (same as den dug in 1979)[2]
1981	
Feburary 13	Mounting attempt followed by scramble and mock flight
16	Coupling of alpha male and subdominant female (2 minutes); upon disengaging female 269 (alpha) runs toward and subdues female
March 15	Den diggings in north end of Hay Camp meadows (4)[2]
	Den diggings in southeast island (2)[3]
23	Den diggings near round meadow (5)[3]; revisted on 28 March
April 11	Two sets of den diggings on south island (6)[3]
	Southeast island den revisited

[1]Den occupied in summer.
[2]Den not occupied in summer.
[3]Summer occupancy unknown.

(Mech and Knick 1978) from 28 January to 4 March, and Isle Royale (Mech 1966; Peterson 1974, 1977, 1979) from 4 February to 2 March. Early studies in Wood Bufffalo National Park (Soper 1942) suggested that the breeding season was restricted to early February. Fuller and Novakowski (1955) reported it occurred during the first three weeks of March.

Seven potential dens were located during late winter (Fig. 31), either from aerial observations of digging, or through ground tracking of wolves. Digging of dens most often occurred after mid-March (Table 23) and most likely reflected an urge by pregnant females to examine potential nursery dens. Digging of potential dens in late winter has also been recorded on Isle Royale (Peterson 1977). The total number of dens possibly visited by wolves was unknown, but only one of the dens (Salt River) known to have been dug out in late winter 1979, 1980 and 1981 was consequently used.

Location of summer homesites in the study area was based on radio tracking, aerial and ground observations of wolves in three localities: Hay Camp-Darough Creek-Raup Lake meadows, Lake Claire meadows, and Lake One meadows.

a. Hay Camp-Darough Creek-Raup Lake meadows

The denning area of the Hornaday River pack in 1978 was located by radio tracking of male U215 and female U262 and their close adherence to the den site locality in April and May (Fig. 22). The den was observed to be in use as early as 20 April, although no pups were seen from the air. Scat at the site in late summer, however, indicated pups had been present. A detailed description of the den site was given in Oosenbrug *et al.* (1980).

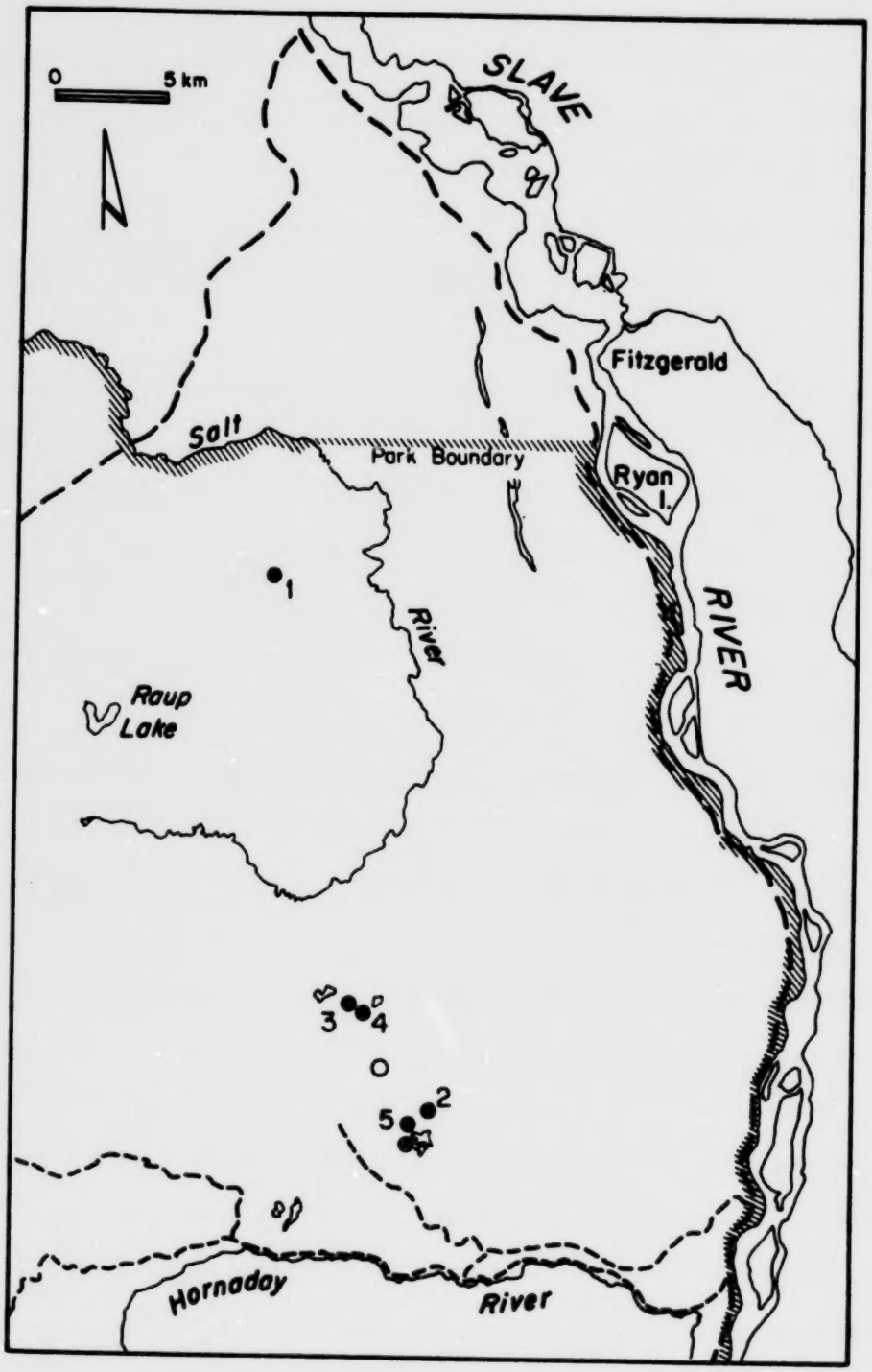


Figure 31. Location of dens observed during late winter, 1979-1981. (O marks the location of the Hornaday River pack den occupied during summer 1978. Numbers refer to names in Table 23.)

Although three potential denning sites for the Hornaday River pack were located by aerial observations during late winter 1978-79 (Fig. 31), none of these was occupied by the pack during summer 1979. One of the sites visited in winter was the den occupied in 1978.

With the exception of female 269 (Fig. 22), radiolocations during May and early June were not clustered for any of the instrumented wolves, suggesting that they were not necessarily associated with a denning site. Three locations for 269 on 22, 30 May and 6 June from the same vicinity in the Hay Camp meadows suggested a possible denning area, but subsequent movements and close ground examination of the area in August revealed no sign of denning activity.

One of the instrumented Hornaday River pack wolves (male 283-4) was believed to be a dominant, or possibly alpha animal, and therefore was expected to be associated with a denning group. However, locations were infrequent during May and early June, and aerial locations of male 283-4 (Fig. 19) showed no evidence of concentrated activity in any one locality.

No intensive ground investigations were carried out in the Hay Camp-Darough Creek meadows during the summer, therefore little is known about denning and rendezvous site activity of the Hornaday River pack during 1979. Contact with a pack in the area was not established until 25 August, when the howls of 2-3 adults and at least four pups were recorded at Darough Creek on the loop road 25 km south of Hay Camp (Fig. 32).

During the intensive monitoring of the Hornaday River pack in February and March 1979, a den digging near one of the tributaries of the Salt River was observed from the air (24 February) and confirmed on the ground (6 March). On 16 May a light coloured wolf was observed lying in

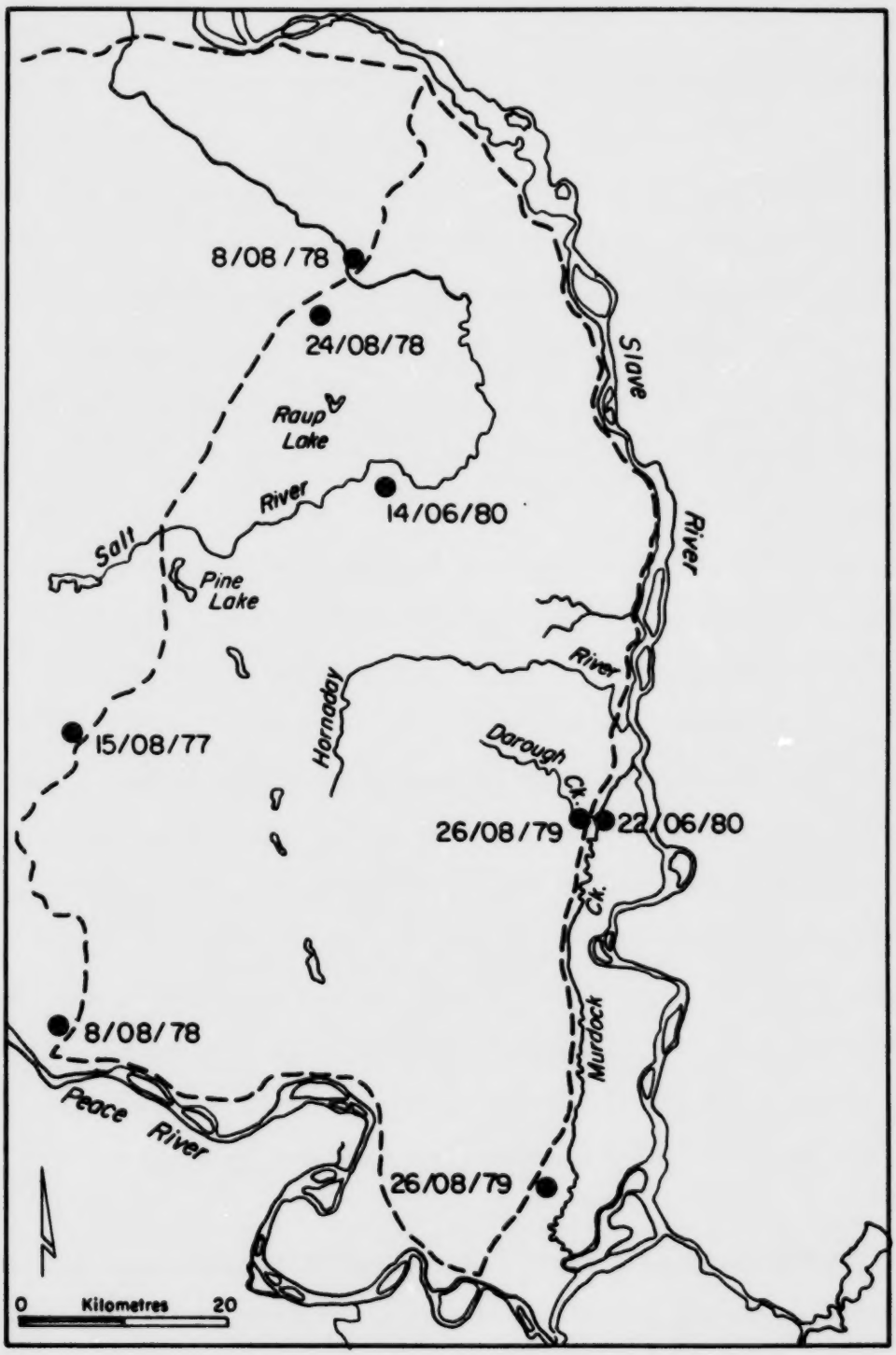


Figure 32. Location of wolf-family units in summer, as determined by evoked howling responses, 1977 to 1980, Wood Buffalo National Park.

front of the main entrance of the den. A ground examination of the denning site by wardens D. West and C. Toews on 18 July confirmed that the den had been occupied in 1979. Descriptions of dens found in 1978-79 were recorded earlier in Oosenbrug et al. (1980).

In summer 1980, two radio locations and limited ground observations provided little information on denning activity of the Hornaday River pack in 1980. Pups were known to have been present in the area, however, as both adults and pups (number undetermined) responded to howls on two occasions on 14 June and 22 July (Fig. 32). One potential den site (Fig. 31) was superficially examined in summer 1981 (G. Haynes, pers. comm.), and no recent activity was noted, and possible occupation of four other potential den sites was not determined.

b. Lake Claire meadows

The den site occupied by the Lake Claire pack in 1978 was observed by radio tracking in late winter of one of the pack members, male U271, and its six consecutive locations in the vicinity of Sweetgrass Island in May and early June (Fig. 22). One of the other wolves in the Lake Claire pack radio tracked throughout summer 1978 was located repeatedly in the Lake One meadows (Fig. 22), and was apparently associated with a denning group in this locality (see below). Locations and site characteristics for dens in the Lake Claire and Lake One meadows are described in Oosenbrug et al. (1980b).

Radiolocations for members of the Lake Claire pack in summer 1979 suggested a concentration of activity in the vicinity of the 1978 denning site on the north shore of Lake Claire (Fig. 22), but no consecutive series of radio locations on one or more of the instrumented wolves in a

restricted area was obtained during May and June. The north shore of Lake Claire was visited on foot in early August, and the 1978 den and vicinity searched for signs of recent wolf activity. The 1978 den was not occupied during 1979 and no other dens were found, although at least five members (four instrumented) of the Lake Claire pack were seen on the ground in the area on 5-6 August (G. Haynes, pers. comm.).

Members of the Lake Claire pack, including pups, occupied the vicinity of Halfway Meadow, approximately 15 km north of Lake Claire, from the middle of July to early August (Fig. 22). Aerial observations of the pack in this locality (10 adults, 4 pups) were made by wardens on bison surveys on 20 and 24 July 1979 (R. Loranger, pers. comm.). On the evening of 6 August the howls of 3 adults and 3-4 pups were recorded at Halfway Meadow, and the following day a rendezvous site at the north end of the meadow was found. Three pups were observed at the rendezvous site, although no adults were present.

It appears likely that considerable movement occurred between Halfway Meadow and Lake Claire, as the adults observed at Lake Claire on 5 August were probably associated with the rendezvous site at Halfway Meadow and possibly the Lake One meadows.

c. Lake One meadows

Throughout the duration of the study it was not possible to determine the exact affiliation of the wolves at Lake One with those in the Lake Claire pack, although in each summer from 1978 to 1980, wolves originally captured in the vicinity of Lake Claire in 1978 and 1979 were present at Lake One. This is to be expected, as bison herds leave Lake One in the fall and only bulls remain behind.

Male U270 traveled north from Lake Claire into the Lake One meadows during April 1978, and remained in the vicinity of Lake One until at least late July. As a result of ground searches of the areas, an active den was located at the northern edge of the large meadow (Fig. 33) on 18 June 1978. An undetermined number of pups was inside the den at this time, however, from 10 July to 12 August, a maximum of six pups were observed at the only identified rendezvous site. At least one pup perished (carcass found in the meadows) prior to the latter date, so there may have been more pups present at the den in June.

During summer 1979 several homesites were located at Lake One (Fig. 33). On 28 July an active rendezvous site was found immediately south of the southeast corner of the large meadow, this site had been occupied recently but not for an extended period of time, probably from 25-28 July. On 29 and 30 July four adult wolves and four pups were observed in the southeast corner of the meadow.

On 6 September the 1979 nursery den of the Lake One wolves was discovered, the following day another larger and more extensively used rendezvous site was located in this corner of the meadow. From the signs of intensive trampling and numerous well worn trails, we assumed that this rendezvous site had been in use for much of August, and probably into early September as well.

On 23 September another den was found on one of the dune ridges approximately 500 m northwest of the nursery den. We do not know the occupancy dates or this den, but believe it was probably occupied sometime between the use of the first den and first rendezvous site (early July?).

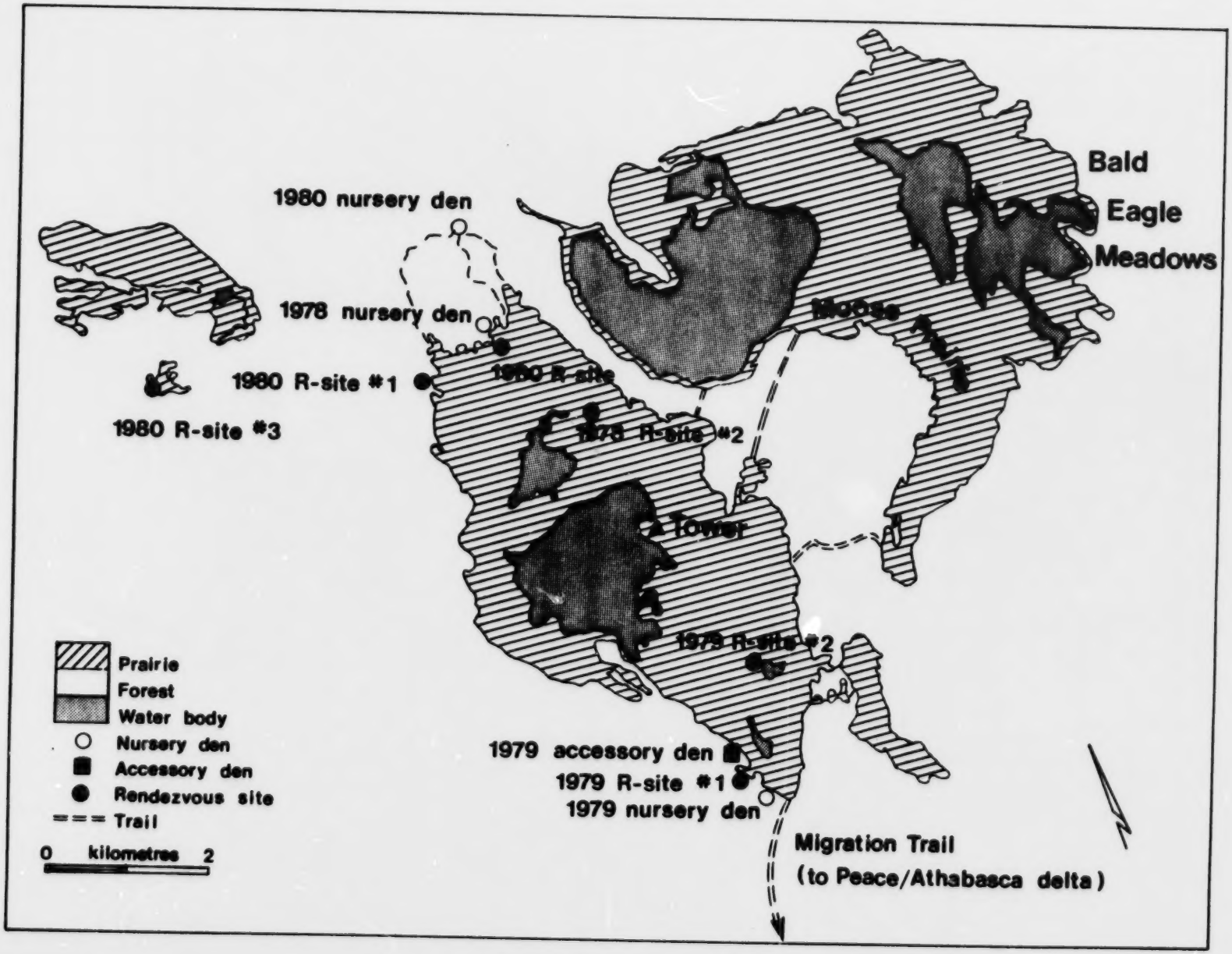


Figure 33. Location of denning and rendezvous sites at Lake One; summers 1978, 1979, and 1980.

Descriptions and scat collections of each of the 1979 homesites are presented in Oosenbrug et al. (1981).

Six pups were observed at the nursery den of the Lake One wolves on 10 June 1980. Three rendezvous sites were occupied from approximately 19 June to 11 July, 12 to 22 July and 22 July to 23 August (Carbyn et al. 1981). In all years pups and adults left the rendezvous sites sometime during mid to late August, and were subsequently observed in or heard from various portions of the Lake One meadows. The entire pack apparently vacated the Lake One meadows as early as the first week in September, but returned at irregular intervals until at least mid-October when observations ceased.

7. Sources of mortality

Changes in pack sizes from early to late winter were not apparent for the Hornaday River pack during the study, rather pack numbers fluctuated throughout the winter. Identification of pups in winter 1978-79 and 1979-80, and the rather stable pack size of 10-14 wolves in both winters, suggested that mortality and/or dispersal must have been operative throughout the year. Observed numbers in the Hornaday River pack decreased to eight animals in the fall of 1980. No pups were identified in winter 1980-81, and it is conceivable that these and other pack members may have existed as a non-instrumented unit in the southeast portion of the winter range established by the pack during 1979-80. During this study mortality in wolves resulted from hunting and trapping, accidents, intraspecific aggression, pup mortality, and possibly disease (Appendix 4).

a. Human harvest

Hunting and trapping of wolves in Wood Buffalo National Park have been carried on since 1926; fur harvest figures from 1950 to 1981 (Fig. 34) indicate that an average of 12 wolves was taken annually during this time. Up to 1975 these figures were necessarily low, since they reflected only wolves sold in the park area; pelts sold on southern markets went largely unrecorded (Church 1976). As well, until 1975 the Northwest Territories offered a forty dollar bounty on wolves. Before 1970 this amount was greater than the dealer's price for the pelt, therefore it seems likely that many park wolves killed in Alberta were taken into the Territories for bounty payment.

It is also possible that some Alberta park trappers may at times submit wolf pelts in arrangement with Northwest Territories non-park trappers to the NWT Wildlife Service in Fort Smith. The Northwest Territories collects no fur tax, and usually pays the trapper on the spot. Park wolves then would go unrecorded; however, this practice does not seem to occur often (D. Anions, pers. comm.). A certain number of pelts are bartered locally or used privately for garments, but this would account for a minimal number of wolf pelts.

Wolf harvest figures since 1975 have been determined by examination of yearly written declarations submitted by trappers at the time of permit renewal, as well as records of local fur buyers and both the Northwest Territories Wildlife Service and Alberta Fish and Wildlife Service. Pelts taken in the Territories section of the park are sent by the Wildlife Service to fur auction houses in Edmonton and the numbers recorded and sent to park headquarters. The park Warden Service collects a fur tax on pelts

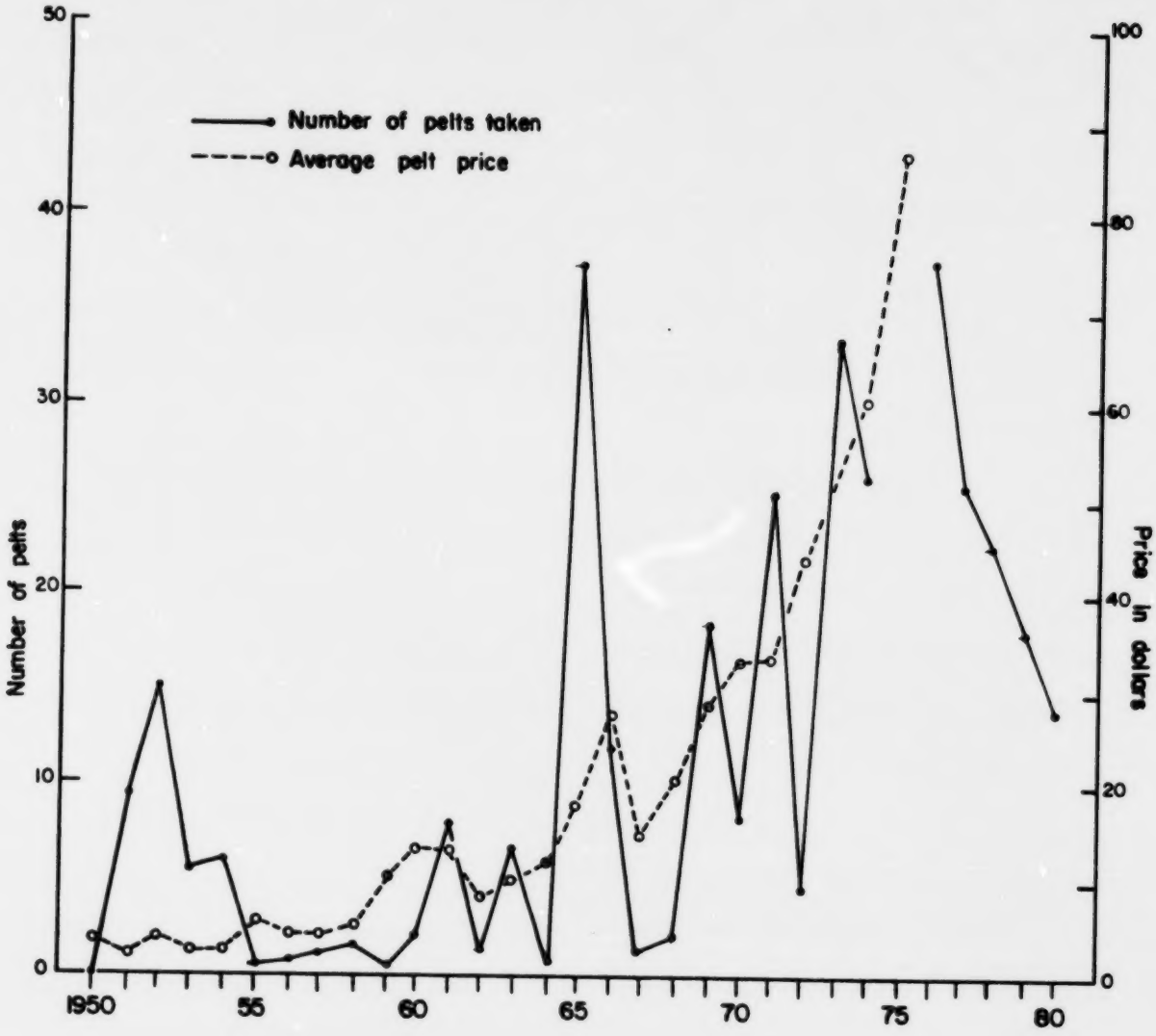


Figure 34. Wolf pelt harvest in Wood Buffalo National Park, 1950-51 to 1980-81, and mean yearly pelt market value (from Church 1976 and Park Warden files).

taken in the Alberta section as a favour to the Alberta Fish and Wildlife Service, which in turn provides records for all pelts sold in Edmonton. In addition, all furs leaving Fort Smith (Northwest Territories) require an export permit for sale in Alberta; these are also dispensed by the Warden Service.

Known records of wolf harvest and population estimates (Table 9) indicate that trapping of wolves in the park continues to be relatively light. It is possible a large number of wolves may have been taken in the years 1973-74 and 1974-75 (Fau 1975), but the wolf population was considered higher during those years than at present. Recent high fur prices and increased illegal use of snow machines, particularly in the open Peace-Athabasca delta region where access is much better than in areas north of the Peace River, may have made wolves a more desirable fur species. The fur harvest records, however, do not really bear this out.

Although some trappers have been successful at trapping wolves in and around the periphery of the park (one trapper snared more than 20 wolves adjacent to the Salt River between 1978 and 1981), most do not actively trap wolves because they are difficult to catch (Soper 1945; Novakowski 1958a) and prices for wolf pelts are still relatively low compared with fine furs such as lynx and fox. In some cases native trappers refuse to trap or kill wolves because of traditional beliefs.

Four instrumented wolves were killed in snares between 1977-78 and 1980-81. It was not practical to correlate trapping of instrumented wolves to the entire park population due to small sample size. Collar returns indicated that trapping mortality for instrumented wolves did not exceed 8% in any year (Table 24), assuming other sources of mortality occurred in the

Table 24. Mortality of instrumented wolves, as determined from recovery of radio-collars, 1978-1981; Wood Buffalo National Park.

	1977-78	1978-79	1979-80	1980-81
Wolves instrumented	21	15	6	1
Losses				
Trapping	1	-	-	3
Intraspecific strife	-	-	2	-
Disease[1]	-	1	-	-
Other	-	-	-	-
Wolves present[2]	21/20	35/34	40/38	39/36
Percent mortality	4.8	2.9	5.0	7.7

[1]Cause of death not verified; wolf suffered from advanced stage of mange in late March 1979.
[2]Pre-mortality figures followed by post-mortality figures.

observed magnitude based on collar recovery. No doubt natural mortality, other than that indicated by collar returns as failure of radio collars, was common. Instrumented wolves may have been caught by trappers and not reported, thereby increasing the proportion of wolves killed. However, on the basis of 12 wolves killed per year out of an estimated mean population of 170 (Table 9), trapping mortality of wolves appeared to account for no more than 7% annually.

The effect of hunting and trapping on wolf productivity and population structure has been discussed by Pimlott et al. (1969) and Van Ballenberghe et al. (1975). These authors felt that exploitation led to increased numbers of pups in the population, but neither gave conclusive reasons for the observed increases. Van Ballenberghe et al. (1975) noted that a greater percentage of adult females that in harvested populations, and Van Ballenberghe and Mech (1975) proposed a direct relationship between food supply and pup survival. Similar relationships between pup proportions and level of exploitation were reported earlier in Wood Buffalo National Park (Fuller and Novakowski 1955, whereby pups increased from 20, to 35, to 53% from 1951-52 to 1953-54 (n = 79) in an experimental wolf control program) on barren-ground caribou ranges in the Northwest Territories (Kelsall 1968), and in Alaska (Rausch 1967).

Haber (1977) speculated that harassment of packs from aerial hunting in Alaska could result in splitting of packs into separate hunting units, each with its own functional response and reproductive performance, thereby effectively increasing wolf predation. It is possible that a stable prey base, a harvested stable wolf population, and increased prey/wolf ratio might result in higher pup survival. Simultaneous conditions of stability,

however, rarely exist for wolves and their prey, and to date no data on the subject are available.

Evidence cited for increased pup numbers (compensatory reproduction) related to levels of harvesting appears to be inconclusive, as the harvest methods used are known to select for young animals. Therefore, a high number of pups in the harvest sample may simply indicate the age class most vulnerable to trapping and poisoning, rather than its actual occurrence in the population. Studies in which selection for certain age classes was minimal, i.e. aerial capture or hunting (Van Camp 1980; Ballard et al. 1981; and this study) do not support the general hypothesis that increased pup proportions exist in exploited populations.

b. Disease

The impact of disease or parasite related mortality on wolf populations is largely unknown. The effects of the mite or mange has been identified as a possible important contributing factor to canid mortality in western North America (Murie 1944; Cowan 1947, 1951; Green 1951; Todd et al. 1981). We examined seven of 43 wolves which showed varying degrees of mange infection (Appendix 4), from localized areas of hair loss to more extensive areas with accompanying skin sores and crusts. During late winter 1979 we captured two wolves out of a pack of seven near Basil Lake. Four pack members, when observed from the air, showed complete hair loss on the tail as well as areas on the neck, shoulders and rump. One of the captured wolves suffered only minor hair loss from the shoulders and rump, while the other had complete hair loss on the tail and abdomen, as well as sores and crusts on the abdomen. Judging from their size and weight, both

wolves seemed to be in good condition despite an abnormally cold winter that year. The lesser infected animal, however, died the following summer, although it was impossible to determine the cause of death from portions of the recovered carcass.

Todd et al. (1981) postulated that occurrence of mange in wolves was most prevalent during periods of high wolf numbers (density dependent), and primarily affected young animals in the population. Wolves increased rapidly in Alberta in the late 1960s (Stelfox 1969), and seemed to have peaked in the early 1970s; 33% of wolves (n = 30) taken at poison stations in 1969-70 in west-cental Alberta had mange. Although there is no documented evidence that mange was prevalent during high wolf numbers in Wood Buffalo National Park during the early 1970s, it is possible that the sharp decline of wolves in 1974-75 was in part due to mange infection. Reports by park trappers in 1980-81 and several observations of mange affected wolves near Fort Smith in summer 1981 suggested that the disease may also be common in a moderately low wolf population in the Wood Buffalo National Park area.

Diseases, such as rabies (Rausch 1969), canine distemper (Choquette and Kuyt 1974; Carbyn 1982), oral papillomatosis (Samuel et al. 1978), brucellosis (Neiland 1974) and tuberculosis (Carbyn 1982), implicated in wolf mortality were not documented in this study. A suspected outbreak of rabies in Alberta in 1952 (Ballantyne 1956) led to wolf control programs there and in Wood Buffalo National Park from 1952 to 1956.

c. Accidents

Mortality from traumatic injuries was reported for two wolves in 1980 (Appendix 4); both were killed by vehicles. One of the wolves was

skinned and examined and also found to have been shot through the neck. Evidence of traumatic injuries in wolves resulting from encounters with large herbivores, trap damage, and intraspecific aggression have been reported by Mech (1970), Murie (1944), Rausch (1966), Stephenson and Johnson (1973) and Neilsen (1977). The small number of carcasses we examined exhibited few signs of injuries other than those inflicted by conspecifics.

In two instances canine teeth in older wolves were broken, similar to results from Alaska (Neilsen 1977) and Slave River lowlands (Jalkotzy, pers. comm.) where the incidence of traumatic injuries increased with age. Examination of 88 wolf carcasses in the Slave River lowlands indicated that 38% of these had been injured (Jalkotzy, pers. comm.) compared to 51% in Alaska (Neilsen 1977), and 10% in Minnesota (Van Ballenberghe 1975). Although they could not all be identified as prey inflicted, these injury rates may to some degree reflect the relative danger of encounters with bison, moose and white-tailed deer, respectively.

Two incidents of wolves escaping with a trap on one of their feet were recorded in the study. Unless these wolves were able to free themselves from such an encumbrance, it is likely their chances of survival would be reduced. Trappers in the park, however, feel that wolves are extremely persistent in chewing at traps, and will wear out the springs in order to escape. Stephenson and Johnson (1973) reported observations of surviving wolves with missing feet and legs, most likely trap inflicted, and Carbyn (1980) reported cases of traps and snares attached to wolves in Riding Mountain National Park. Two wolves captured during this study had

previously been caught in a snare, as evidenced by wounds or portions of the snare still attached.

One of the instrumented wolves, (male 323) was caught in a leg-hold trap in late February 1980 and released, and managed to survive the winter despite a noticeable limp. A considerable portion of its recovery period was spent scavenging on two bison carcasses. Limping wolves were also observed in the Hornaday River pack in 1979-80, and at Lake One in summers, 1979, 1980, 1981. Wolves that are hampered in their travel with packs may be left behind, as was the case for wolf 323 and a pup observed at Lake One in September 1979. These then may have to rely on scavenging and small prey in order to survive. Some partially disabled wolves obviously do survive (see Stephenson and Johnson 1973), as the same limping female was observed at Lake One during two summers (1979, 1980) of field observations.

d. Pup mortality

Mortality of pups has been shown to be an important factor in limiting wolf populations (Pimlott et al. 1969; Van Ballenberghe et al. 1975), although the proximate causes and timing are still largely unknown. The carcass of a three month old pup which may have died from starvation, was found at a rendezvous site at Lake One during the summer of 1978. Another emaciated carcass of what seemed a 4-6 month old pup was found in December 1978 at Hay Camp. Pup mortality has been linked to food supply (Van Ballenberghe and Mech 1975) and probably applied to these two instances. Three other juvenile wolves died as a result of wounds inflicted by other wolves (Appendix 4).

C. Bison

1. Numbers and distribution

Total numbers of bison in Wood Buffalo National Park since 1972 have been determined annually from fixed-wing aerial surveys conducted by the park Warden Service, and the results were summarized by Carbyn and Anions in prep.). The apparent stability of the park population in recent years (1975-1984) contrasts with that in the adjacent Slave River lowlands, where numbers have decreased steadily from approximately 1700 in 1971 (Rippin 1971) to 360 in 1981 (V. Hawley, pers. comm.).

Historical migration patterns of bison in Wood Buffalo National Park were described earlier (Oosenbrug et al. 1980a). In the area north of the Peace River (Area I) most bison normally spend the summer in the forested Alberta Plateau region, moving twice-yearly between this area and the winter ranges of the Hay Camp, Darough Creek and Murdock Creek meadows to the southeast. South of the Peace River (Area II) the north shore of Lake Claire is used on a year-round basis, although bison radiate east and south from here during the winter months.

Absolute numbers and locations of all bison in the primary bison ranges north of the Peace River were available from the annual midwinter total counts conducted by the park Warden Service. These results were used to described the year-to-year distributional pattern of bison within the study areas from 1978 to 1981. A comparison of distances from locations in a systematic 300-point grid (see Methods) to the nearest observed bison on each annual survey (Fig. 35) indicated that in midwinter bison were most uniformly distributed in 1980-81 and least in 1978-79.

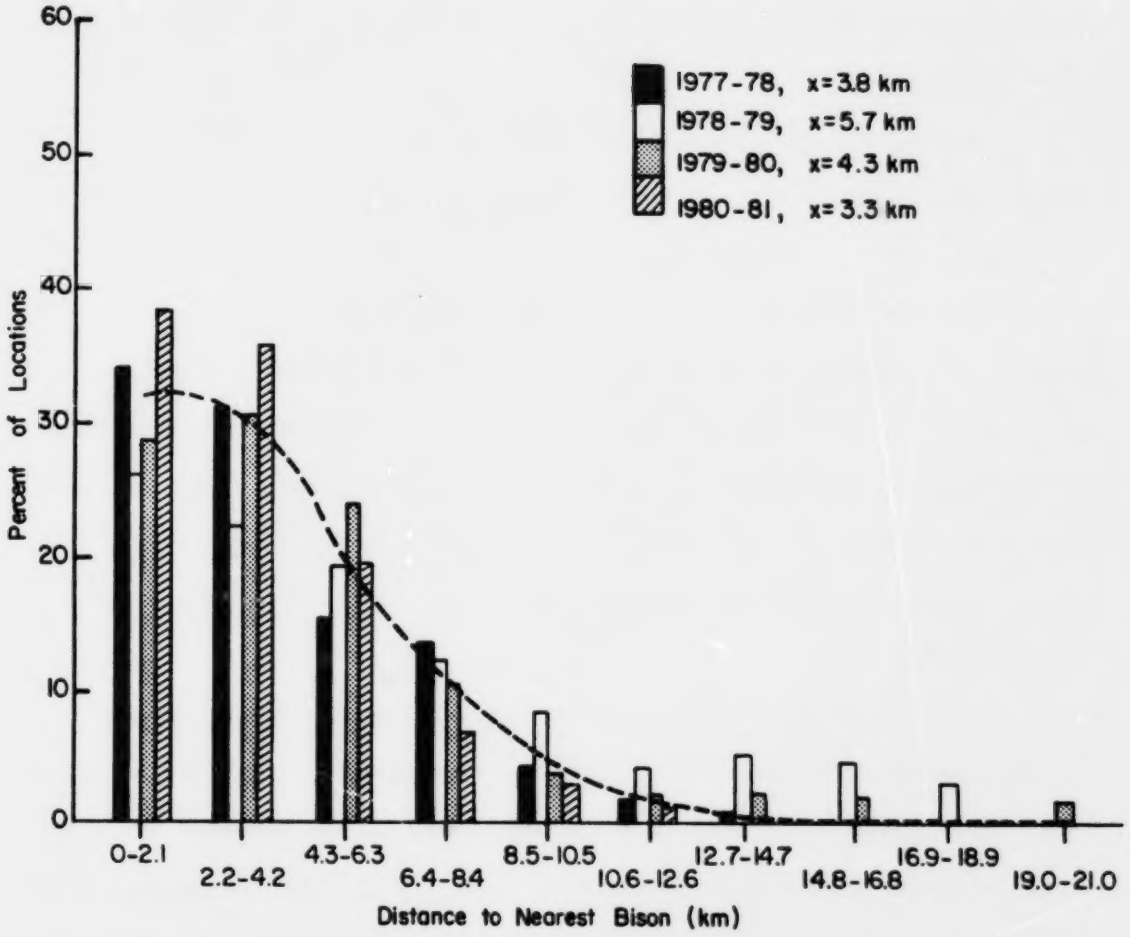


Figure 35. Midwinter distributional pattern of bison in the Raup Lake, Hay Camp, Darough Creek, and Murdock Creek meadows combined, 1977-78 to 1980-81, as determined by the distance of 300 grid locations to the nearest bison in these areas. Bison locations derived from annual midwinter total bison counts. Dashed line represents 1977-78 to 1980-81 mean for each distance grouping.

Mid-month estimates of bison numbers (Fig. 36; Appendix 5) in four geographical localities occupied by the Hornaday River pack from November 1977 to May 1981 (Fig. 37) were calculated from the results of aerial surveys conducted by the wardens and/or S. Oosenbrug. An overview of the results indicated that in terms of both numbers and densities (Figs. 38, 39, Tables 25, 26) the Darough Creek and Hay Camp meadows comprised the most important bison habitat on a year-round basis and over the entire study period.

Seasonal movements and distribution of bison were reflected by changes in numbers from winter to summer in each of the localities (Tables 25, 26 and Appendix 10). Changes in numbers from year to year represented annual shifts from one locality to another, or occupation of habitat outside the home range of the Hornaday River pack. Variations in timing of seasonal movements and occupation by bison of different areas of their range was thought to be largely determined by climatic factors such as freeze-up, spring thaw, water levels and snow-depth (Anions 1980). This behaviour may also have been adaptive to avoid constant harassment from wolf predation.

In late winter 1978-79 bison in the Hay Camp and Darough Creek meadows, mainly small groups or solitary animals, were relatively sedentary. These bison comprised the major prey of the Hornaday River pack until late April, when large mixed herds moved north from the Murdock Creek meadows wintering area. According to park reports (Couchie 1979) these herds vacated the Hay Camp and Darough Creek meadows during December 1978, prior to the deep snows of February and March.

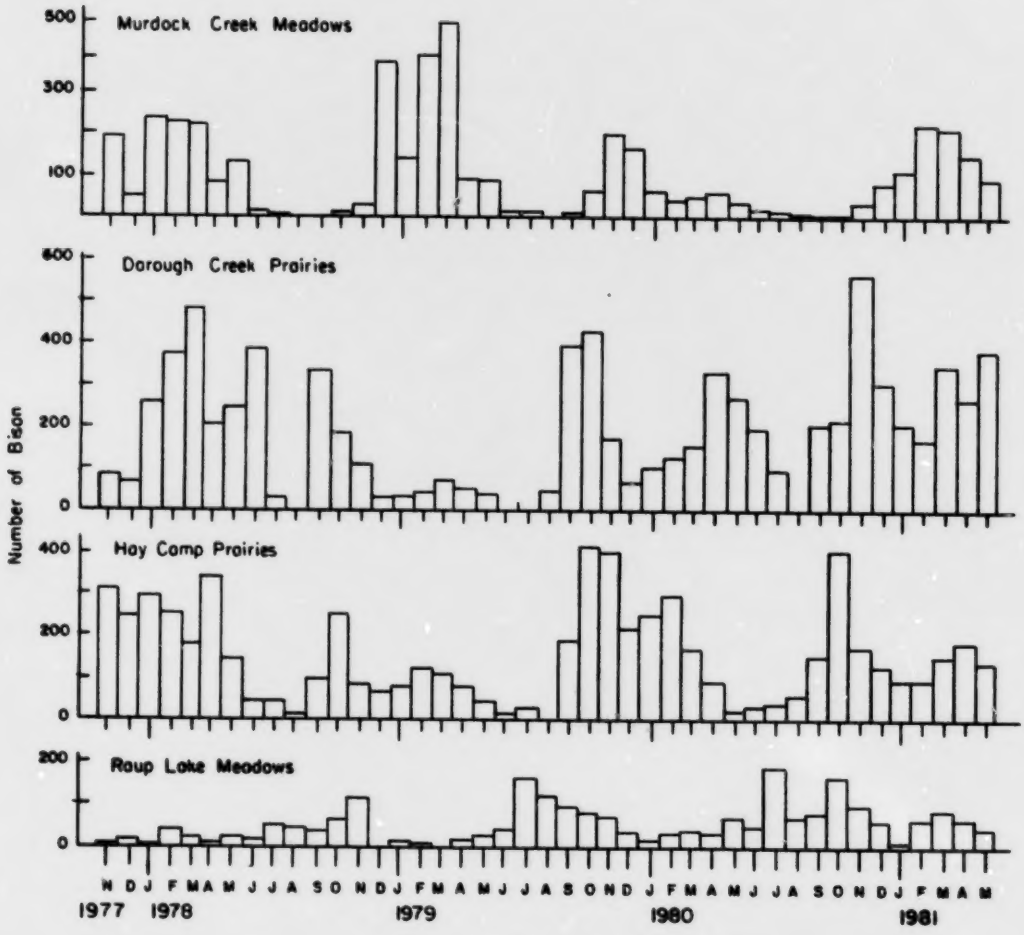


Figure 36. Mid-month estimates of bison numbers in four geographical localities occupied by the Hornaday River pack, Wood Buffalo National Park; 1977 to 1981.

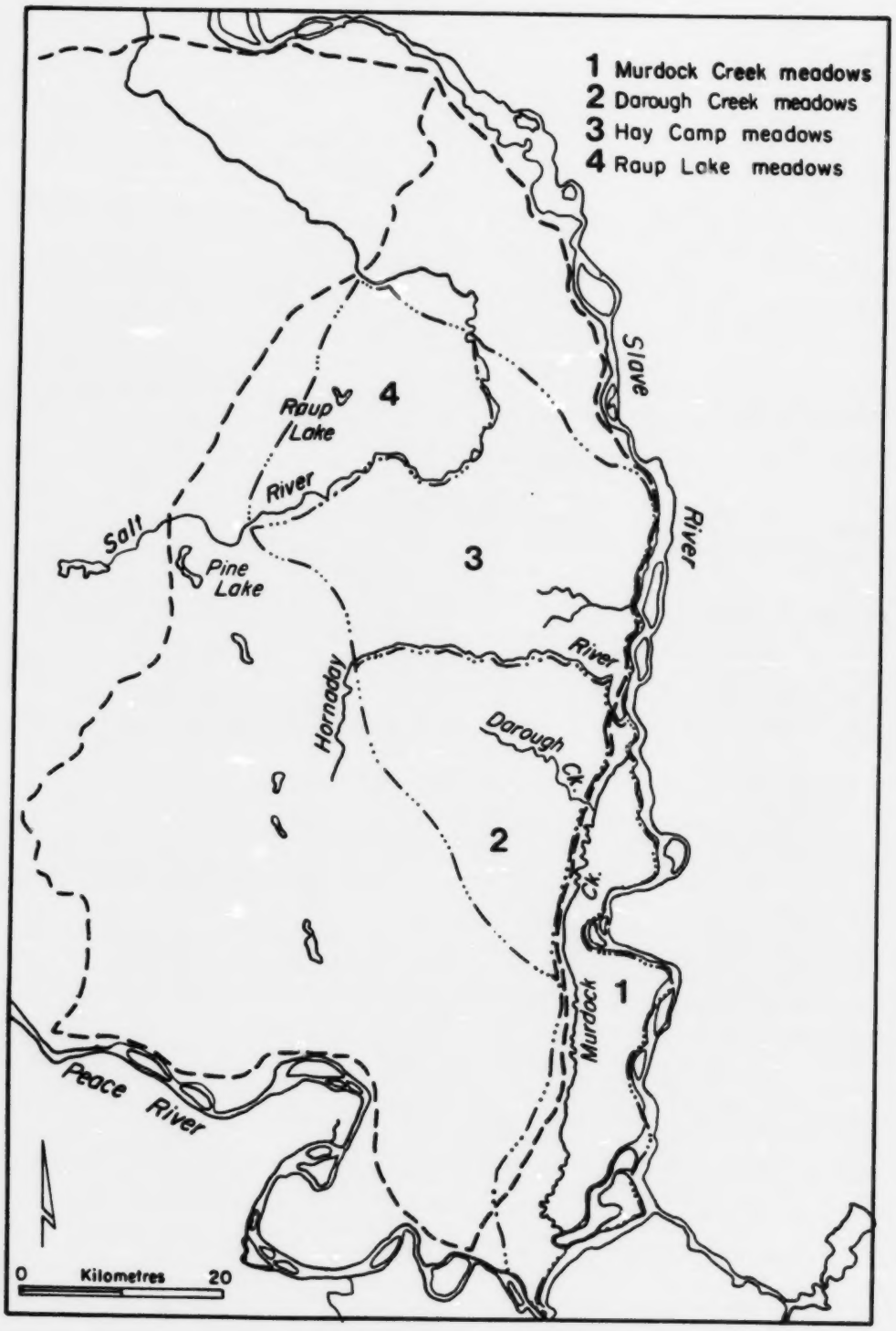


Figure 37. Location of four geographical localities occupied by the Hornaday River pack from 1977 to 1981, Wood Buffalo National Park.

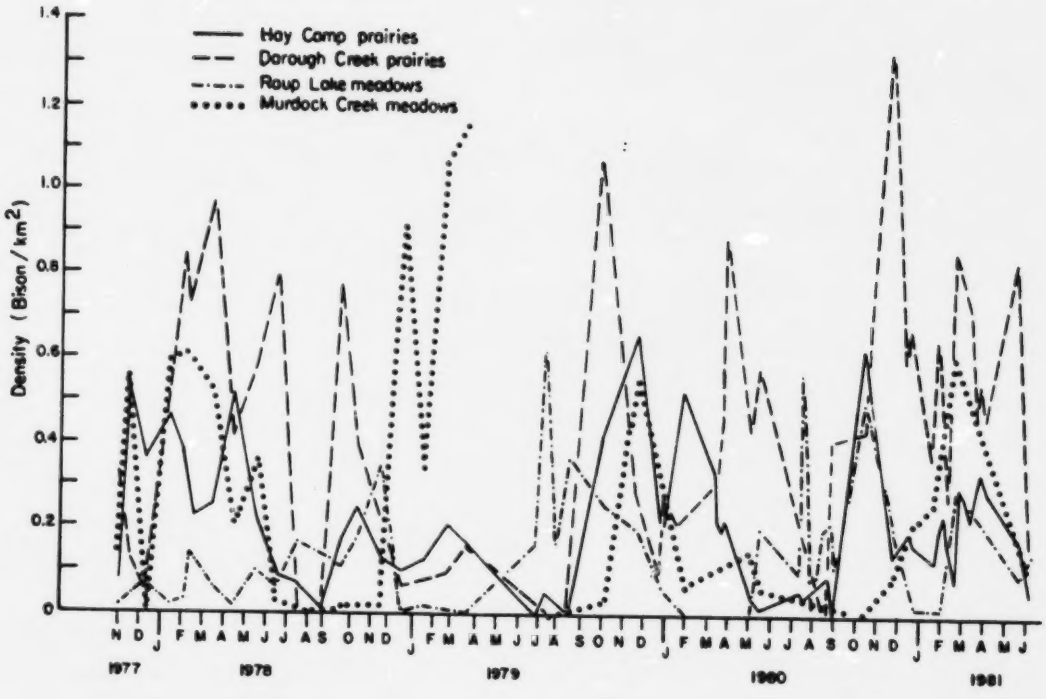


Figure 38. Mid-month estimates of bison density in four geographical localities, as determined from aerial surveys of primary bison ranges, Wood Buffalo National Park; 1977 to 1981.

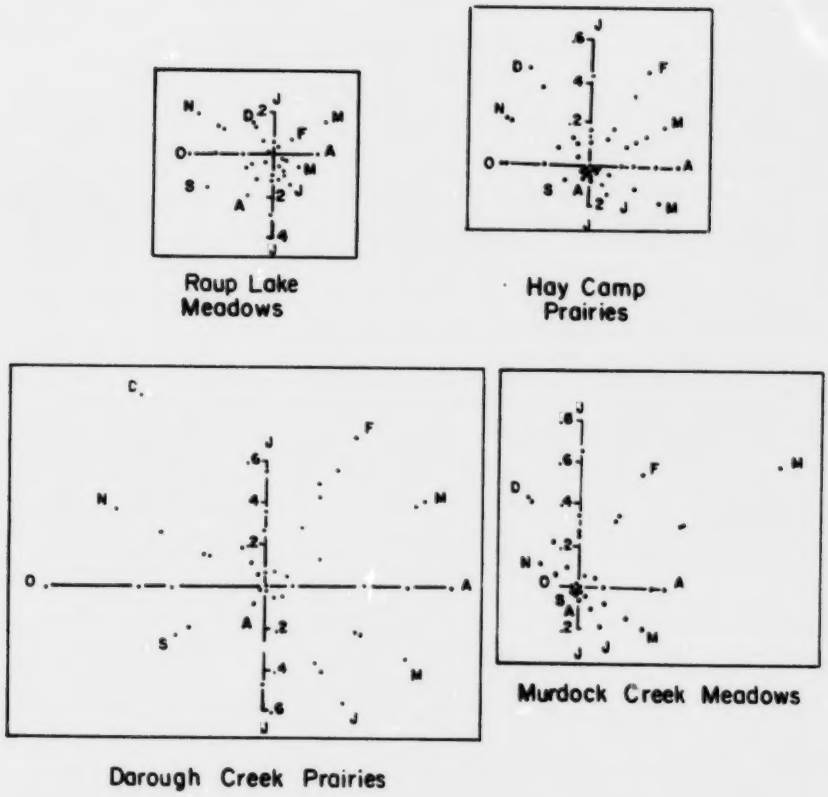


Figure 39. Seasonal pattern of bison density in four geographical localities occupied by the Hornaday River pack, Wood Buffalo National Park; 1977 to 1981.

Table 25. Estimates of mean bison numbers and density on primary bison ranges coincident with the year-round home range of the Hornaday River pack, Wood Buffalo National Park; 1977 to 1981.

Locality	1977-78		1978-79		1979-80		1980-81		1977 to 1981	
	N	D	N	D	N	D	N	D	N	D
Murdock Creek meadows										
Winter	169	.418	248	.612	90	.222	125	.307	158	.390
Summer	27	.066	31	.077	14	.035	-	-	24	.059
Darough Creek meadows										
Winter	246	.497	60	.121	162	.380	307	.723	194	.456
Summer	201	.405	153	.309	166	.389	-	-	173	.407
Hay Camp meadows										
Winter	253	.392	88	.136	232	.359	130	.201	176	.273
Summer	84	.130	94	.146	111	.172	-	-	96	.149
Raup Lake meadows										
Winter	17	.052	23	.069	32	.098	53	.163	31	.095
Summer	41	.125	89	.272	98	.302	-	-	76	.234
Total										
Winter	685	.352	419	.224	516	.276	615	.329	559	.299
Summer	353	.189	367	.196	389	.208	-	-	369	.197

N = numbers; D = density; both determined from mid-month estimates.

Table 26. Estimates of mean bison numbers and density on primary bison ranges coincident with the winter home range of the Hornaday River pack, Wood Buffalo National Park; 1978 to 1981.

Locality	1978-79		1979-80		1980-81		1978-79 to 1980-81	
	N	D	N	D	N	D	N	D
Murdock Creek meadows								
Early winter	199	.491	174	.430	51	.126	141	.348
Midwinter	268	.662	48	.119	155	.383	157	.388
Late winter	277	.684	48	.119	168	.415	164	.405
Darough Creek meadows								
Early winter	72	.169	121	.285	431	1.014	208	.489
Midwinter	41	.096	119	.280	189	.445	116	.273
Late winter	67	.158	245	.576	302	.711	205	.482
Hay Camp meadows								
Early winter	73	.113	304	.471	141	.219	173	.268
Midwinter	102	.158	269	.417	87	.135	154	.237
Late winter	105	.163	123	.191	161	.250	130	.202
Raup Lake meadows								
Early winter	56	.172	50	.154	57	.175	54	.166
Midwinter	4	.012	22	.068	32	.098	19	.058
Late winter	8	.024	30	.092	69	.212	36	.111
Total								
Early winter	400	.222	649	.361	680	.378	576	.320
Midwinter	415	.231	458	.254	463	.257	445	.247
Late winter	457	.254	446	.248	700	.389	535	.297

N = numbers; D = density.

During most winters a number of bison cross back and forth on the Peace River ice near Scow Channel. In some years this may involve as many as 500-800 animals (Kuyt 1971; Tempany and Cooper 1976a; Carbyn and Anions in prep.). We suspect that most of these are mixed herds of primarily cows and calves, and thus their distribution may significantly alter the available prey base in Area I winter ranges, where total numbers rarely exceed 1000 bison.

In 1977-78, 1978-79, and 1979-80 the migration of approximately 200 bison (based on track counts and observed herds) occurred from the Murdock Creek area south across the Peace River into Area II during December and January. On 15 March 1978 two distinct trails crossing the Peace River at Scow Channel and Sweetgrass Landing indicated the northward movement of bison from the Peace-Athabasca delta into Area I. In 1978-79 due to a late spring, northward migration did not begin until late March, and tracks again indicated that movements had taken place across the Peace River. Approximately 170 bison were believed to have crossed at Scow Channel into Area II in December 1979 (Couchie 1979), and at least 100 bison were known to have gone north across the river again in early February 1980.

It is not known whether deep snow hampered movements of herds in 1978-79. Fuller (1966) reported that herds were more mobile in deep snow than individual bison, in that the animals followed in file from one feeding area to another, thereby reducing overall energy expenditure. Observations in 1979-80 and 1980-81 suggested that these groups were capable of moving quickly from one locality to another through all types of terrain and snow cover. The causes however, unless they are as obvious as an attack by wolves, remain obscure and cannot be answered until this

aspect of the biology of the species is given proper attention, and that unfortunately was outside the scope of this study.

2. Herd size and structure

On the basis of aerial observations of bison from 1971 to 1981, mean annual herd size in Area I was approximately 16, and the herd sizes were somewhat larger (25) in Area II (Table 27). Seasonal mean herd size appeared to be more variable in Area I, being largest in early winter, and smallest in summer, while mean herd size in Area II apparently remained similar throughout the year. Ground observations at Lake One during summers 1978 to 1980 indicated that the largest herds in that area occurred in midsummer (July-August) prior to and during the rut (Oosenbrug et al. 1981; Carbyn et al. 1981). However, these observations may have simply reflected patterns of use at that particular locality.

Mean herd size in winter was more variable in Area I than in Area II (Fig. 40), and these changes were related to relatively large-scale movements of bison back and forth across the Peace River. Noticeable examples occurred in February 1981 and February 1976. In 1976, emigration of a large number of mixed herds with calves from the Hay Camp Darough Creek-Murdock Creek meadows resulted in a mean herd size of five bison, mostly consisting of singles or small groups of bulls (Tempany and Cooper 1976a). Similar conditions existed in the winter of 1978-79 (Oosenbrug and Carbyn 1982).

The sex ratio of adult bison south of the Peace River, as determined from ground observations in summer at Lake One, was close to 1:1 (Table 28). Data for Yellowstone bison (Meagher 1973) indicated a slight

Table 27. Mean herd size, determined from aerial observations of bison in primary bison ranges of Wood Buffalo National Park; 1971-1981.

Year	Late winter (15 Jan.-30 March)		Spring (16 Apr.-15 June)		Late summer (1 Aug.-30 Sept.)		Early winter (15 Oct.-31 Dec.)		Annual mean[2]	
	Area I	Area II	Area I	Area II	Area I	Area II	Area I	Area II	Area I	Area II
1971	30	36							30	36
1973		53[1]				43[1]				
1975	25	37					29	16	27	27
1976	5	28							5	28
1977	17	21							17	21
1978	10						37[1]		10	
1979	9				29[1]	43[1]	23	24	18	24
1980	14	24			14	27	24	21	17	24
1981	20		9		11				13	
Seasonal mean[2]	16	29	9		13	27	25	23	16	25

[1]Mixed herds with calf components only.
[2]Excludes mixed herds with calf components only.

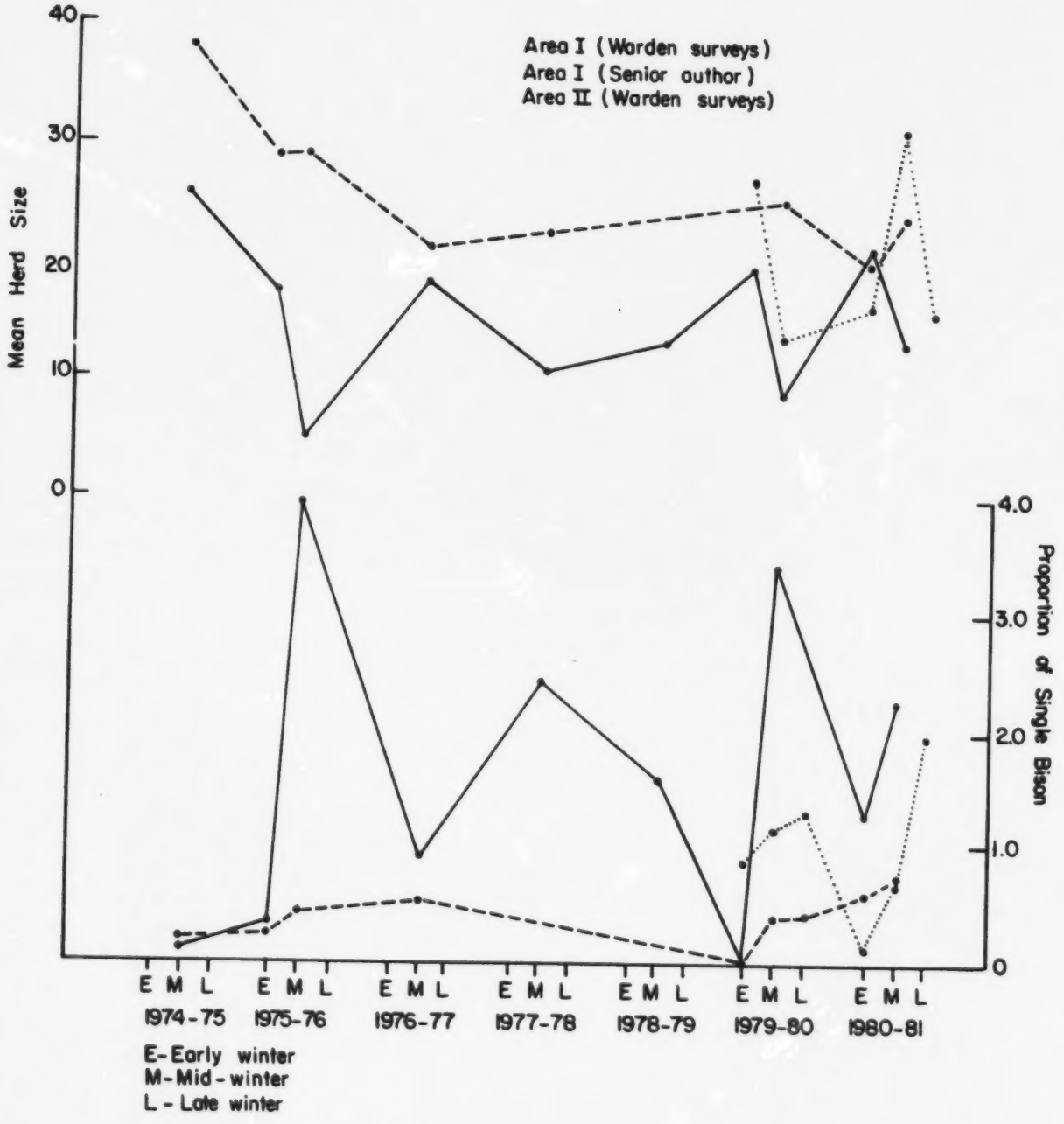


Figure 40. Mean herd size and proportion of single bison in early, mid, and late winter, as determined from aerial surveys of primary bison ranges in Wood Buffalo National Park; 1974-75 to 1980-81 by wardens and by research team.

Table 28. Sex ratios for adult[1] bison at Lake One, Wood Buffalo National Park; summers 1978, 1979 and 1980.

Month	1978		1979		1980		1978-1980		Bull:cow ratio
	Bulls	Cows	Bulls	Cows	Bulls	Cows	Bulls	Cows	
May	-	-	222	32	50	58	272	32	3.0:1
June	71	76	291	209	182	352	544	637	0.9:1
July	472	406	570	335	21	77	1063	818	1.3:1
August	308	408	-	-	60	84	368	492	0.7:1
September	62	134	87	169	4	3	153	306	0.5:1
October	133	329	91	15	-	-	224	344	0.7:1
Total	1046	1353	1261	760	317	574	2624	2687	1.0:1

[1]Excludes calves and yearlings.

preponderance of males, whereas Fuller (1960) and Van Camp and Calef (1980) reported greater proportions of females in the bison populations in Wood Buffalo National Park and adjacent Slave River lowlands. However, herd units without calves, based on the number of observations of solitary bison (primarily bulls), were considerably more common and variable in Area I than in Area II (Fig. 40; Table 29).

Since mean productivity in both areas was similar (Table 30), but survival not necessarily so, the greater proportion of non-calf units in Area I may have been more related to the segregation of the sexes in that the tendency of single bulls and small bachelor herds to be separated from mixed herds with calves may have been caused by the terrain in Area I. The meadows north of the Peace River are less extensive than those in the Peace-Athabasca delta, and are often interspersed by large stands of forest, which may facilitate separation of bulls from the more mobile cow-calf herds. An exodus of cow-calf herds in winter 1975-76 and 1978-79 (see above) resulted in primarily adult bulls being left behind in the Murdock Creek, Darough Creek and Hay Camp meadows, considerably altering the prey-base composition available to wolves in those winters.

3. Reproduction and calf survival

A review of bison productivity data from 1951 to 1975 (Tempany 1976) concluded that the late summer (August/September) number of calves in Wood Buffalo National Park was between 10 and 20% of the total population. Systematic surveys of calf production and survival since 1975 (Table 31) support Tempany's conclusions. Fuller (1966) reported a combined calf crop of 15-20% and estimated that the bison were producing calves at the rate of

Table 29. Seasonal and annual proportion of single bison in population samples of bison determined from aerial observations in Wood Buffalo National Park; 1971-1981.

Year	Late winter (15 Jan.-30 March)		Spring (16 Apr.-15 June)		Late summer (1 Aug.-30 Sept.)		Early winter (15 Oct.-31 Dec.)		Annual mean	
	Area I	Area II	Area I	Area II	Area I	Area II	Area I	Area II	Area I	Area II
1971		8.0					6.3	6.0	6.3	7.0
1975	3.4	5.6							3.4	5.6
1976	20.0	12.3							20.0	12.3
1977	15.9	12.5							15.9	12.5
1978	24.0								24.0	
1979	22.3					12.0	1.5	0.0	10.2	6.0
1980	18.5	12.1			33.2	8.0	19.8	14.2	23.8	11.4
1981	20.2		34.3		38.5				31.0	
Seasonal mean	17.3	10.1	34.3		35.9	10.0	9.2	7.1	19.8	9.1

Table 30. August calf proportions determined from visual observations and photo analysis on aerial bison surveys in Wood Buffalo National Park, 1975-81.

	Area I			Area II		
Year	Calves	Total herd	Percent calves	Calves	Total herd	Percent calves
1975	247	1347[1]	18.0	126	797	15.8[2]
1976	128	1257[1]	10.2	162	1121	14.5[2]
1977	97	1116[1]	8.7	118	937	12.6
1978	32	190	16.8	165	1148	14.3
1979	31	257	12.1	100	1069	9.4
1980	112	716	15.5	107	706	15.2
1981	25	140[1]	17.9	-	-	-
Mean	672	5023	13.4	778	5778	13.5

[1]Visual count only.
[2]Photo count only; excludes non-calf herds and solitary bison.

Table 31. Bison reproduction and calf survival in Wood Buffalo National Park, based on best counts from aerial bison survey in primary ranges of Area I and Area II; spring 1975 to 1981 (adapted from Warden Service files).

Calf cohort	Spring (May/June)			Late summer (August/September)			Early winter (November)			Late winter[1] (February/March)			Spring following[1] (May/June)		
	Sample size	Calves Number	%	Sample size	Calves Number	%	Sample size	Calves Number	%	Sample size	Calves Number	%	Sample size	Calves Number	%
1975	4341	512	11.8	2174	374	17.2	5414	775	14.3	3904	570	14.6	1139	149	13.1
1976	-	-	-	2378	290	12.2	2274	240	10.6	2422	214	8.9	801	67	8.4
1977	2007	341	17.2	2053	215	10.5	1360	152	11.2	482[3]	62	12.9	609	62	10.2
1978	1283[2]	189	14.7	1338	197	14.7	1617	171	10.6	2184	231	10.6	-	-	-
1979	-	-	-	1326	134	10.1	3049	269	8.8	704[3]	43	6.1	-	-	-
1980	2819	485	17.2	1434	222	15.5	4003	454	12.1	4750	470	9.9	-	-	-
Total	10450	1527	14.6	10703	1431	13.4	14730	1722	11.7	14446	1590	11.0	2549	278	10.9

[1]Late winter and spring following are new yearling percentages of total numbers minus young-of-year (calves).
[2]Area I data only.

two calves per mature cow every three years, i.e. - at conception the cow; calf ratio was approximately 1.5:1. Fuller reported a noticeable difference between calf proportions in the Peace-Athabasca delta and areas north of the Peace River during 1950-53, although his methods of data collection were different in each area. Results for 1975 to 1981 indicated similar calf production in the two areas (Table 30) and thus we pooled these data (Table 31). Proportion of calves in summer has been reported for bison in Yellowstone (10-20%; Meagher 1973), and Slave River lowlands (15-20%; Van Camp and Calef, in prep.).

The conception rate of bison in Wood Buffalo National Park was not determined during this study, however, Fuller (1966) noted approximately 67% of the cows older than three years were pregnant (53% for all cows older than one year). Although conception rates in Yellowstone from 1964 to 1966 were even lower (52%), these rates are considered low for the species. Both Fuller and Meagher presented a variety of reasons for these observed rates, including a high proportion of aged females in the population, diseases such as brucellosis, winter severity, and delayed conception due to lactation. Van Camp and Calef (in prep.) concluded that a preponderance of old females, as well as a low number of mature males, were primarily responsible for the poor breeding success of bison in the Slave River lowlands. Yet their proportions of calves in summer were similar to those in W.B.N.P.

We suspect that disease, winter severity, aging of the population and delayed conception were factors in lowering breeding success for bison in the park. We observed breeding behaviour throughout the year, and newborn calves in every month except January, although like Fuller (1966)

we suggest that the height of the rutting season is in late July and early August, and most calves are subsequently born in late May and early June.

If the conception rate reported by Fuller (approximately 53% for all females older than yearlings) and summer survival rates of calves (August cow/calf ratio) at Lake One (29% for 1978 to 1980 combined) are correct, then nearly one-half of the calves conceived died in utero or as neonates between February and August. This type of early calfhood mortality has been reported for a small sample by Meagher (1973:62) who assumed a calf mortality rate of 46% from winter to spring for 28 mature cows trapped and released in Yellowstone National Park during 1964-65. Novakowski (1959a) calculated that approximately 50% of calves in a sample of 164 cows in Wood Buffalo National Park were lost prior to or shortly after parturition. Potential calf production has been reported by Fuller (1966) and Van Camp and Calef (1980), and generally exceeded our observed 13.5% August calf proportions by 5-10%. This difference is most likely a result of some form of neonatal mortality - possibly disease, inclement weather, or predation, that occurs between birth and August.

Although each year's actual calf crop is unknown, estimates of calf proportions in the park during late summer are considered the most representative of annual calf production (Anions 1980, Carbyn and Anions in prep.) since most of the calving has taken place by then. Surveys flown since 1975, in November and February (see Table 31), have indicated an average decrease of approximately 1% per month in calf proportions (winter 1977-78 was excluded due to possible observation errors and incomplete sampling). These rates are somewhat less than a monthly 2% decrease in calf proportions from June to December for park bison during 1951-54

(Fuller 1966) and 1.3% calf crop decrease per month observed in the Slave River lowlands during winters 1975-78 (Van Camp and Calef in prep.).

Using general survey data the mean late-winter proportion of calves from 1975 to 1981 was 10.6% ranging from a low of 6.1% in 1979 to 14.6% in 1975 (Table 31). Data for 1949 and 1951 suggested that calf proportions were approximately 6-8% in late winter, down more than 50% from summer (Fuller 1966). Calf proportions in the Slave River lowlands during late winter averaged 3.6% from 1973 to 1978, although prior to these years they were similar to the park figures.

Fuller (1966) observed little calf mortality after late winter and believed that calf survival to the yearling stage was practically synonymous with recruitment into the breeding population. Our data support his conclusions, as representation of yearlings in the late summer sample at Lake One (Table 32) was similar to that in late winter for all primary winter ranges of bison. However calves born in a summer following a more severe winter, i.e. 1978-79, appeared to suffer greater mortality during their first winter than calves born after a mild winter (Tables 31, 32), resulting in depressed yearling numbers the following summer. Low late winter calf numbers were possibly a direct result of a previous severe winter, but may also have been aggravated by increased wolf predation on calves.

Table 32. Bison herd composition at Lake One, based on classified counts of identified herds; summers 1978, 1979, and 1980.

	Total sample size	Percentage composition[1]				Cow:calf ratio
		Bulls	Cows	Calves	Yearlings	
May						
1978	-	-	-	-	-	-
1979	260	85.4	12.3	1.9	0.5	6:1
1980	146	34.2	39.7	5.5	21.8	7:1
June						
1978	185	38.4	41.4	12.4	9.3	3:1
1979	547	53.2	38.2	4.8	4.1	8:1
1980	694	26.2	50.7	9.5	15.0	5:1
July						
1978	1048	45.0	38.7	8.0	10.0	5:1
1979	1059	53.8	31.6	7.5	7.7	4:1
1980	124	16.9	62.1	8.9	13.3	7:1
August						
1978	957	32.2	42.6	11.9	15.1	4:1
1979	-	-	-	-	-	-
1980	179	33.5	46.9	15.6	4.7	3:1
September						
1978	248	25.0	54.0	15.7	6.3	3:1
1979	290	30.0	58.3	6.6	5.7	9:1
1980	10	40.0	30.0	20.0	12.5	-
October						
1978	594	22.4	55.4	14.8	8.7	4:1
1979	113	80.5	13.3	3.5	2.6	4:1
1980	-	-	-	-	-	-
Total						
1978	3032	34.5	44.6	11.8	11.2	4:1
1979	2251	56.0	33.8	5.9	5.2	6:1
1980	1153	27.5	49.8	10.0	14.2	5:1

[1]Figures based on total sample size, except for yearlings which were based on total sample size minus calves (see Oosenbrug *et al.* 1980b, 1981 and Carbyn *et al.* 1981 for actual numbers).

D. Predator-prey relations

1. Relationship between wolf and bison distribution

a. Patterns of wolf-bison association

The Hornaday River pack spent most of each winter 1977-78 to 1980-81 within a 650 km^2 home range core (Fig. 27, Table 21). The pack's usual distribution thus coincided with two important portions of the primary bison ranges north of the Peace River - the Hay Camp and Drough Creek meadows (Fig. 41). The relationship between wolf distribution and bison abundance within four localities most frequently occupied by the Hornaday River pack from 1978-79 to 1980-81 was determined from 237 radiolocations (97% of all radiolocations) (Table 33).

On the basis of relative abundance in all winters, the Hay Camp, Darough Creek and Raup Lake meadows were disproportionately occupied by the Hornaday River pack. This pattern was particularly evident in winter 1978-79, when the pack spent 88% of its time in the Hay Camp and Darough Creek meadows, despite unusually high numbers of bison in the Murdock Creek meadows (Table 33). Bison abundance and pack distribution appeared most closely related in 1979-80, although during that winter areas outside the four localities (i.e. Peace-Athabasca delta) were temporarily occupied in January.

Relative bison abundance varied during 1978-79 to 1980-81 from 21% to 44% and 14% to 50% in the Hay Camp and Darough Creek meadows (Table 33), respectively. However, occupation by the Hornaday River pack of these areas remained relatively constant (38-48% in 1978-79 and 35-40% in 1980-81). This was not the case for the Murdock Creek and Raup Lake meadows, where occupation by the pack varied from winter to winter (see below).

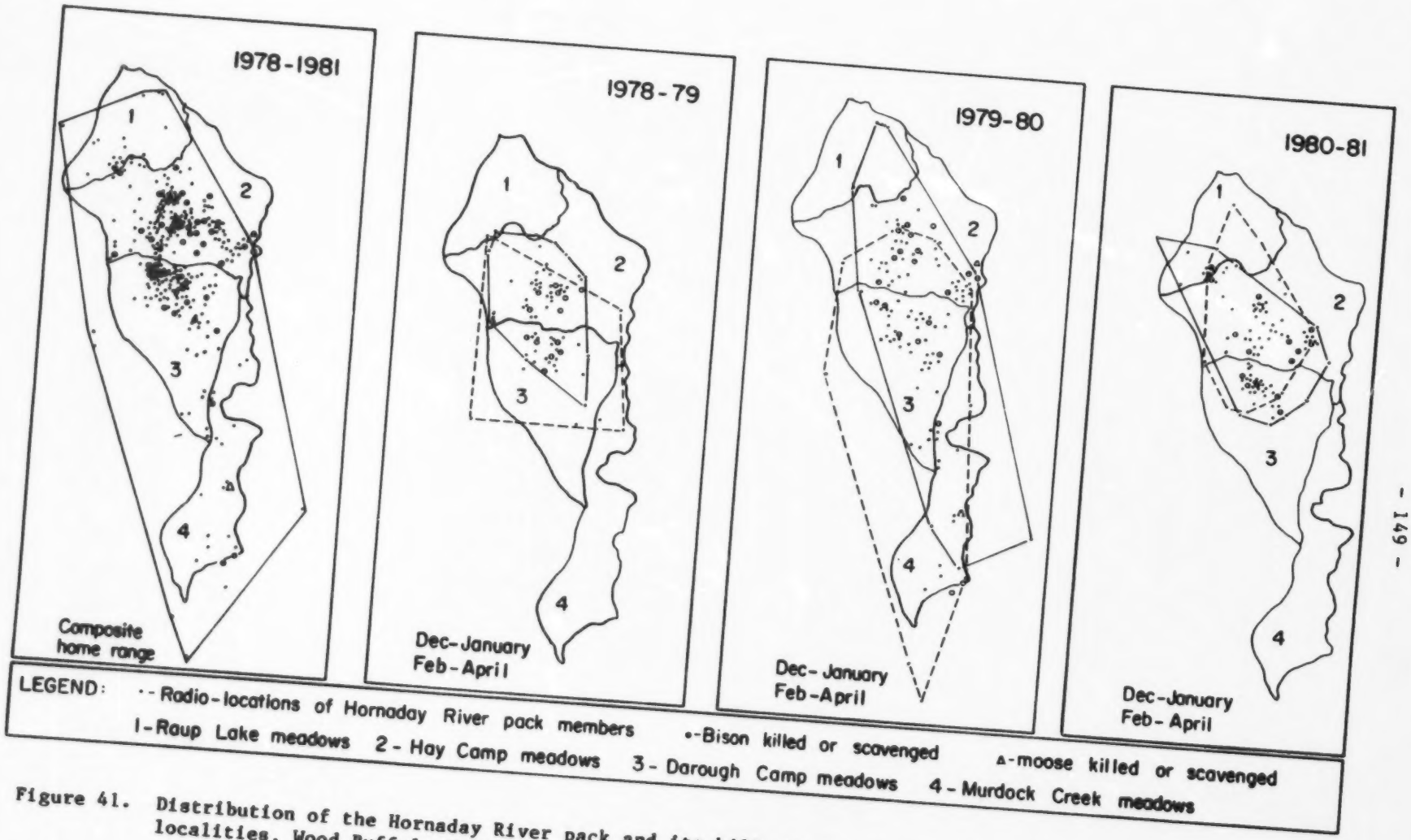


Figure 41. Distribution of the Hornaday River pack and its kills in and adjacent to four geographic localities, Wood Buffalo National Park; winters 1978-79 to 1980-81.

• Radiolocations of Hornaday River pack members ◦ Bison (• moose) killed or scavenged
1 = Raup Lake meadows, 2 = Hay Camp meadows, 3 = Darough Creek meadows, 4 = Murdock Creek meadows.

Table 33. Relationship between bison abundance and distribution of the Hornaday River pack, winters 1978-79 to 1980-81, Wood Buffalo National Park.

Month	Totals		Percent of total bison and radiolocations for Hornaday River pack									
			Hay camp meadows		Darough Creek meadows		Murdock Creek meadows		Raup Lake meadows		Areas outside	
	Bison	Radio-locations										
1978-79												
November	339	-	24.8	-	32.7	-	9.4	-	33.0	-	-	-
December	458	1	13.3	100.0	7.0	0.0	79.7	0.0	0.0	0.0	-	0.0
January	260	6	30.8	0.0	14.2	66.7	53.1	16.7	1.9	0.0	-	16.7
February	568	11	21.6	18.2	7.9	54.5	69.9	0.0	0.5	27.3	-	0.0
March	640	24	16.1	70.8	11.6	25.0	72.5	4.2	0.0	0.0	-	0.0
April	241	8	32.0	50.0	24.5	50.0	37.3	0.0	6.2	0.0	-	0.0
Total	2506	50	21.1	48.0	14.3	40.0	59.3	4.0	5.6	6.0	-	2.0
1979-80												
November	831	1	47.8	100.0	20.8	0.0	23.3	0.0	8.1	0.0	-	0.0
December	466	21	45.1	28.6	14.8	38.1	33.0	28.6	7.1	0.0	-	4.8
January	430	14	57.7	42.9	25.3	0.0	14.7	35.7	2.3	0.0	-	21.4
February	484	27	59.9	48.1	26.7	22.2	6.6	25.9	6.8	0.0	-	3.7
March	393	29	41.0	31.0	39.7	62.1	10.9	0.0	8.4	6.9	-	0.0
April	497	10	16.9	20.0	67.2	60.0	10.7	0.0	5.2	20.0	-	0.0
Total	3101	103	44.8	37.9	31.3	35.5	17.4	17.5	6.5	3.9	-	4.9
1980-81												
November	833	1	19.0	0.0	66.5	0.0	3.6	0.0	10.9	100.0	-	0.0
December	524	15	23.5	86.7	58.6	6.7	13.5	0.0	4.4	6.7	-	0.0
January	406	7	21.4	71.4	51.7	14.3	24.9	0.0	1.7	14.3	-	0.0
February	521	24	16.7	41.7	32.2	50.0	40.1	0.0	10.9	8.3	-	0.0
March	773	26	19.1	23.1	44.5	46.2	25.9	0.0	10.5	30.8	-	0.0
April	627	11	27.8	45.4	41.5	27.3	21.7	0.0	9.1	18.2	-	9.0
Total	3684	84	21.1	46.4	50.0	34.5	20.3	0.0	8.6	17.9	-	0.0
1978-79 to 1980-81												
November	2003	2	31.9	50.0	41.8	0.0	12.8	0.0	13.5	50.0	-	0.0
December	1448	38	27.2	57.9	28.2	23.7	40.7	15.8	3.9	2.6	-	2.6
January	1096	27	37.9	40.7	32.5	18.5	27.5	22.2	2.0	3.7	-	14.8
February	1573	62	29.1	40.3	21.7	38.7	40.6	11.3	5.9	8.1	-	1.6
March	1806	79	22.8	40.5	31.8	45.6	39.1	1.3	6.3	12.7	-	0.0
April	1365	29	24.5	37.9	47.8	44.8	20.4	0.0	7.2	17.2	-	0.0
Total	9291	237	29.0	42.6	34.1	36.7	29.8	8.4	7.0	9.3	-	2.9

Although the distribution of the Hornaday River pack in winter was apparently not determined by the relative abundance of bison within its home range, distances between pack locations and the nearest bison (singles and groups combined) were significantly less ($p < 0.05$) in all winters (except 1980-81) than would be expected from a random distribution of 300 location points (Table 34, Fig. 42). This suggests, to varying degrees from year to year, the Hornaday River pack was predictably associated with bison. Aside from 1977-78, where sample size may have been a factor, close association between wolves and bison was most evident in 1978-79 (Table 34), when the pack and small groups of bison were localized in the Hay Camp meadows.

Patterns of day-to-day associaton of wolves and bison could not be determined, but a number of possible factors may have been important for wolves. These included: (1) distribution of vulnerable bison groups, i.e. cow-calf herds, (2) day-to-day movements of these groups, either intrinsic, or in response to harassment by wolves or other external stimuli, i.e. human disturbance, weather conditions, (3) traditional use of familiar terrain, and repeated visits to former kills and potential denning sites, (4) limits imposed by the distribution of adjacent wolf packs, and (5) snow cover conditions.

b. Travel distances by wolves

Distribution of the Hornaday River pack from February to April 1979 was restricted to 420 km^2 within the Hay Camp and Darough Creek meadows, or 15% of the total 2740 km^2 winter range occupied from 1977 to 1981. In December-January 1979-80 this figure increased to 62% and was 56% from February to April 1980. Like 1978-79, occupation by the Hornaday River

Table 34. Actual versus hypothetical mean distance of the Hornaday River pack to the nearest bison, as determined by radiolocations of the pack and annual midwinter total bison counts; Raup Lake, Hay Camp, Darough Creek, and Murdock Creek meadows, Wood Buffalo National Park.

Winter	Mean distance to nearest bison (km)		E/O ratio
	Expected random distribution	Observed Hornaday river pack distribution	
1977-78	3.8 (300)[2]	1.4 (10)	2.7:1
1978-79	5.7 (300)	2.5 (50)	2.3:1
1979-80	4.3 (300)	2.7 (103)	1.6:1
1980-81	3.3 (300)	2.2 (84)	1.5:1
1977-1981	4.3 (1200)	2.5 (247)	1.7:1

[1]Based on 300-point grid (see Methods).
[2]Sample size in brackets.

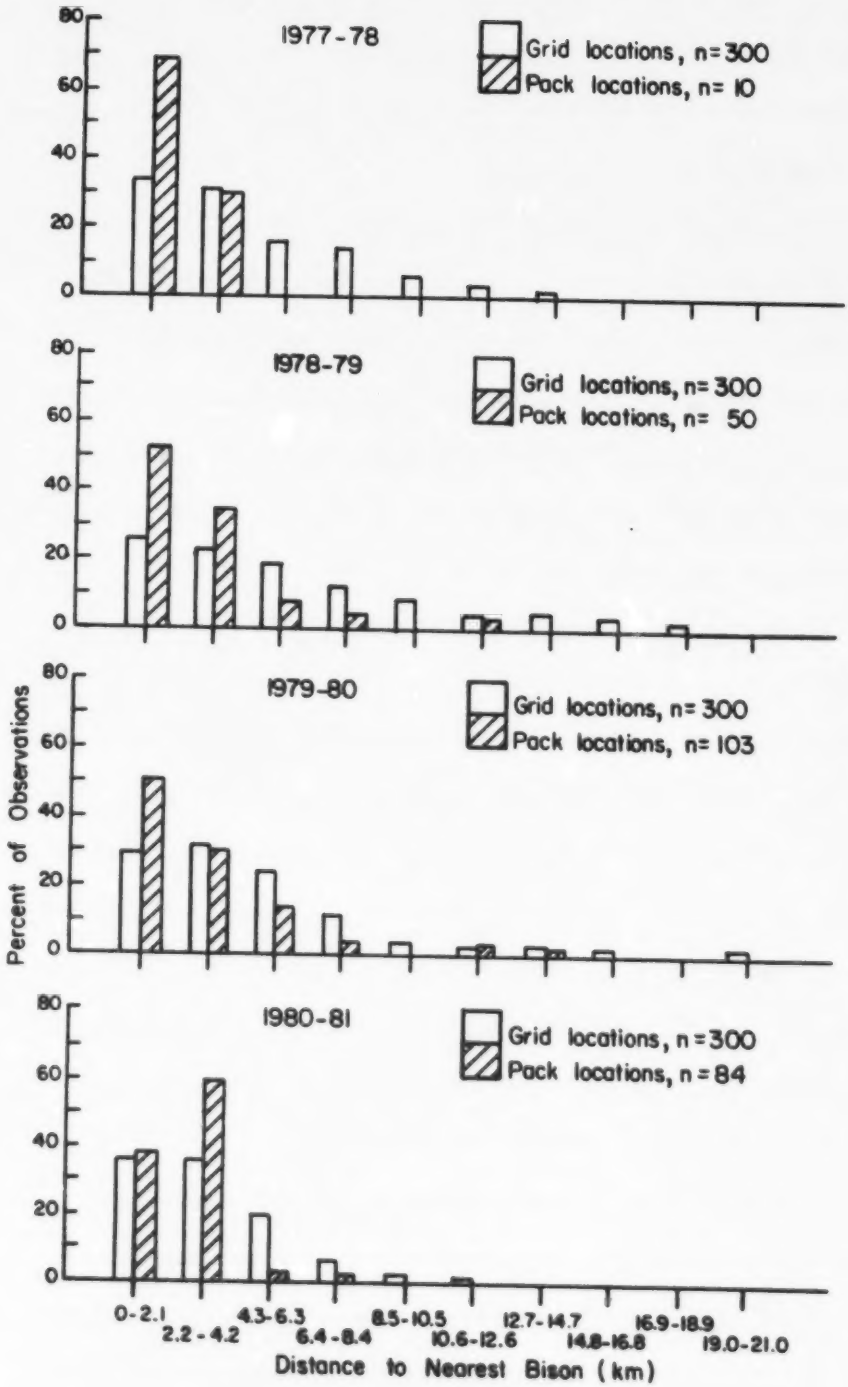


Figure 42. Actual versus hypothetical distances (km) of the Hornaday River pack from the nearest bison, as determined by radiolocations of the pack and annual midwinter total bison counts.

pack of its total winter range was considerably more restricted in 1980-81; the proportion occupied varied from 16% in December-January 1980-81 to 24% from February to April 1981.

Data on movements of the Hornaday River pack (Table 35) indicated that mean daily distances between radio locations were smaller in winters of contracted home range use. They, however, were greater in 1979-80 although observations of activity suggested that in the daytime at least, the pack traveled the least during winter 1979-80 (Table 36). Travel distance generally decreased from early to late winter, with the exception of 1980-81 when snow crust conditions in late winter enabled easy travel for wolves. The pack traveled, rested, or interacted with prey during an average of 25, 25, and 50% of our observations respectively (Table 36).

Late winter reduction of area usage within home ranges, in travel distances, and of observations of travel appeared to be in response to bison movements as well as snow conditions. Aerial surveys of bison in winter have shown that the main bison migrations take place from October to December, and that the animals do not settle into their winter ranges until early or mid-January (Couchie and Collingwood 1978), while snow depth in most years continues to increase throughout the winter and reaches a maximum in late March.

During late winter 1978-79 the Hornaday River pack traveled primarily within the Hay Camp and Darough meadows, with the majority of available prey consisting of adult male bison either in small groups or alone. Adjacent viable packs preyed on overwintering herds in the Salt Plains and Murdock Creek meadows. The Hornaday River pack rarely ventured into these areas. In January 1979-80 the Hornaday River pack traveled more

Table 35. Mean distances[1] (km) between consecutive daily radiolocations of the Hornaday River pack for winters 1978-79 to 1980-81, Wood Buffalo National Park.

Year	Early winter	Midwinter	Late winter	Total
1978-79	-	6.3 (9)	5.3 (29)	5.5 (38)
1979-80	12.0 (25)[2]	11.9 (42)	6.1 (38)	9.8 (105)
1980-81	8.9 (17)	6.0 (34)	9.0 (39)	8.6 (90)
1978-1981	10.7 (42)	8.9 (85)	6.9 (106)	8.3 (233)

[1]In some cases distances were determined over several days.
[2]Number of observation days given in brackets.

Table 36. Activity patterns of the Hornaday River pack in winters 1978-79 to 1980-81, Wood Buffalo National Park.

Year	Total observations	Travel	Rest[1]	Prey interactions[2]
1978-79				
Early winter	-	-	-	-
Midwinter	13	38.5	30.8	30.8
Late winter	32	21.9	34.4	43.8
Total	45	26.7	33.3	40.0
1979-80				
Early winter	16	31.3	31.3	37.5
Midwinter	40	20.0	17.5	62.5
Late winter	37	13.5	27.0	59.5
Total	93	19.3	23.7	57.0
1980-81				
Early winter	15	46.7	33.3	20.0
Midwinter	30	30.0	23.3	46.7
Late winter	32	21.9	15.6	62.5
Total	77	29.9	22.1	48.0
1978-1981				
Early winter	31	38.7	32.3	29.0
Midwinter	83	26.5	21.7	51.8
Late winter	99	19.2	26.3	56.5
Total	215	24.7	25.1	50.2

[1]Excludes resting at kills, carcasses, or near herds.
[2]Includes resting at kills, carcasses, or near herds.

than 40 km in 12 hours into the Murdock Creek meadows, possibly in response to the extensive southward migration of bison herds into that area and across the Peace River into Area II.

Extensive movements of the Hornaday River pack in 1979-80 may not have been entirely food motivated. Unlike the previous two winters, no wolves other than the Hornaday River pack were observed in the Murdock Creek meadows during 1979-80, suggesting that this pack may have been expanding its home range (pack numbers increased from eight to 14 between 1977-78 and 1979-80). In late February the Hornaday River pack had a violent encounter with the neighbouring Salt River pack, which had entered the former pack's home range in search of bison. A month later the Hornaday River pack traveled north to a denning site believed to have been occupied by the Salt River pack in 1979.

The Hornaday River pack remained within its home range core much of the winter 1980-81, and did not venture into the Murdock Creek meadows (Fig. 41). Bison numbers in the Hay Camp and Darough Creek meadows were similar to the previou winter, but pack size was reduced to eight wolves. Based on 1979-80 observations it is possible that the Hornaday River pack split sometime during 1980, with part of it dispersing into the apparently unoccupied Murdock Creek meadows, although we do not have radiotelemetry data in 1980-81 to confirm this suspicion. During the winter 1980-81 the instrumented pack frequented the Raup Lake meadows as much as it did the Murdock Creek meadows in 1979-80, possibly due to the presence of bison herds in this area.

Disperal by members of the Hornaday River and Lake Claire packs into summer ranges has been discussed earlier in this report. The smaller ranges for the latter were attributed to the year-round availability of bison in the Lake Claire region. Wolves in the Hornaday River pack spent early and midsummer in areas generally vacated by cow-calf herds, and members of the fragmented pack likely shifted food habits to smaller prey.

Despite the relatively large home range of the Hornaday River pack (Table 13), comparison of late winter movements of the pack (Table 35) with those from other studies suggested that travel distances of wolves preying on bison were somewhat less than of wolves preying on moose (Mech 1966; Peterson 1977; Fuller and Keith 1980), but more than for wolves preying on deer (Kolenosky 1972) and elk (Carbyn 1980). On Isle Royale a pack of 16 wolves travelled 443 km over 31 days in February and March, or an average of 14.3 km per day (Mech 1966). In Alaska, Burkholder (1959) followed a pack in late winter which averaged 24 km of travel per day for 15 days. Kolenosky (1972) found that a pack of eight wolves in Ontario travelled 327 km over 46 days in mid and late winter, and averaged 7.1 km per day. More recently Peterson (1977) calculated the average travel per day for two packs on Isle Royale in late winter periods for the years 1971 and 1974 as 11.1 km. Fuller and Keith (1980) reported variations in mid and late winter straight line distances for wolves in northern Alberta from 9.0 km in 1977 to 5.7 km per day in 1978, but concluded that actual distances travelled during these years were likely much larger.

Although travel distances for the Hornaday River pack were greatest in 1979-80 (Table 35), actual observations of the pack indicated that the wolves spent less time travelling during the day than in the other winters

(Table 36). This may be partially due to the small proportion of observations made where the pack was traveling in late winter 1980, when bison were abundant and accessible, and predation rates were highest.

Distances traveled between kills were smaller in late winter than in early winter, and averaged 57.5 km over the entire winter from 1978-79 to 1980-81 (Table 37). The mean distance between kills was least in late winter 1979-80 (38.6 km). Fuller and Keith (1980) reported that the average straight line distance between moose kills was 44 km in 1977 and 25 km in 1978. From January to March 1969 wolves travelled an average of 14.7 km between deer kills in Ontario (Kolenosky 1972), and Carbyn (1983) reported a mean distance of 5.1 km between elk kills in Manitoba during a winter of unusually deep snow.

Winter severity seems to have been an important factor affecting activity patterns of the Hornaday River pack. The winter of 1979-80 was somewhat milder than normal, and followed a severe winter in 1978-79. The pack travelled less and killed more frequently in 1979-80 than in 1978-79 or 1980-81. Most of the kills in 1979-80 were of calves (see below), suggesting that these were especially vulnerable, and that their predisposition to wolf predation possibly resulted from poor in utero vigour from the previous winter (Peterson 1977:158).

Greater snow depths in late winter 1978-79 and 1980-81 hampered wolf and bison movements, resulting in more localized predation. Late winter crusting conditions in 1981, however, enabled the pack to forage farther afield. Fuller and Keith (1980) reported that deep snow and cold temperatures resulted in restricted movements of a pack in northern Alberta in winter 1977-78. The greater proportion of observations of a pack

Table 37. Mean distance between kills[1] (km) made by the Hornaday River pack in winters 1978-79, 1979-80, and 1980-81, Wood Buffalo National Park.

	Early winter			Midwinter			Late winter			Total		
	Total distance	Number kills	Distance between kills	Total distance	Number kills	Distance between kills	Total distance	Number kills	Distance between kills	Total distance	Number kills	Distance between kills
1978-79	-	-	-	107.1 (17)	2	53.6	164.3 (31)	4	41.4	271.4 (48)	6	45.2
1979-80	528.0 (44)	7	75.4	511.7 (43)	9	56.8	231.8 (38)	6	38.6	1271.5 (125)	22	57.8
1980-81	204.7 (23)	2	102.4	264.0 (44)	5	52.8	405.0 (45)	7	57.9	873.7 (112)	14	62.4
Total	732.7 (67)	9	81.4	882.8 (104)	16	55.2	801.1 (114)	17	47.1	2416.6 (285)	42	57.5

[1]Calculated from mean daily travel distances and predation rates for each winter period. Number of days radio-tracking shown in brackets.

travelling in 1980-81 may also have been a reflection of improved condition of bison after a previous mild winter, or changes in the social structure of the pack resulting in a less experienced hunting unit.

c. Distribution of wolf-killed bison

The geographic distribution of kills made by the Hornaday River pack (Fig. 43), like that of the distribution of the pack itself, was not directly related to the relative abundance of bison within the pack's home range (Table 38). One shift in kill distribution in another study was attributed partially to an increased occurrence of moose in northern Alberta (Fuller and Keith 1980), but this was not noted in our study. The distribution of kills appeared to be more closely related to the movement of the pack and suggested that predation was heaviest in the pack's home range core (Fig. 43). Kills there comprised 93, 68, and 73% of the total kills recorded in winters 1978-79, 1979-80, and 1980-81, respectively.

2. Wolf-bison behavioural interactions

a. Wolf hunting strategy and success

A total of 65 wolf-prey encounters was observed from aircraft in Wood Buffalo National Park during the four winters 1977-78 to 1980-81. Sixty-three of these were of wolves and bison, and two of wolves and moose. In 29 of the wolf-bison encounters the wolves merely watched their prey, and in another 18 the wolves approached their prey, but did not attack (Table 39). The wolves attacked on 17 occasions, and were successful in killing a target animal on three occasions.

Wolves concentrated primarily on herds (56 of 63 observations). Differences in prey targets between winters 1978-79 and 1980-81 were not

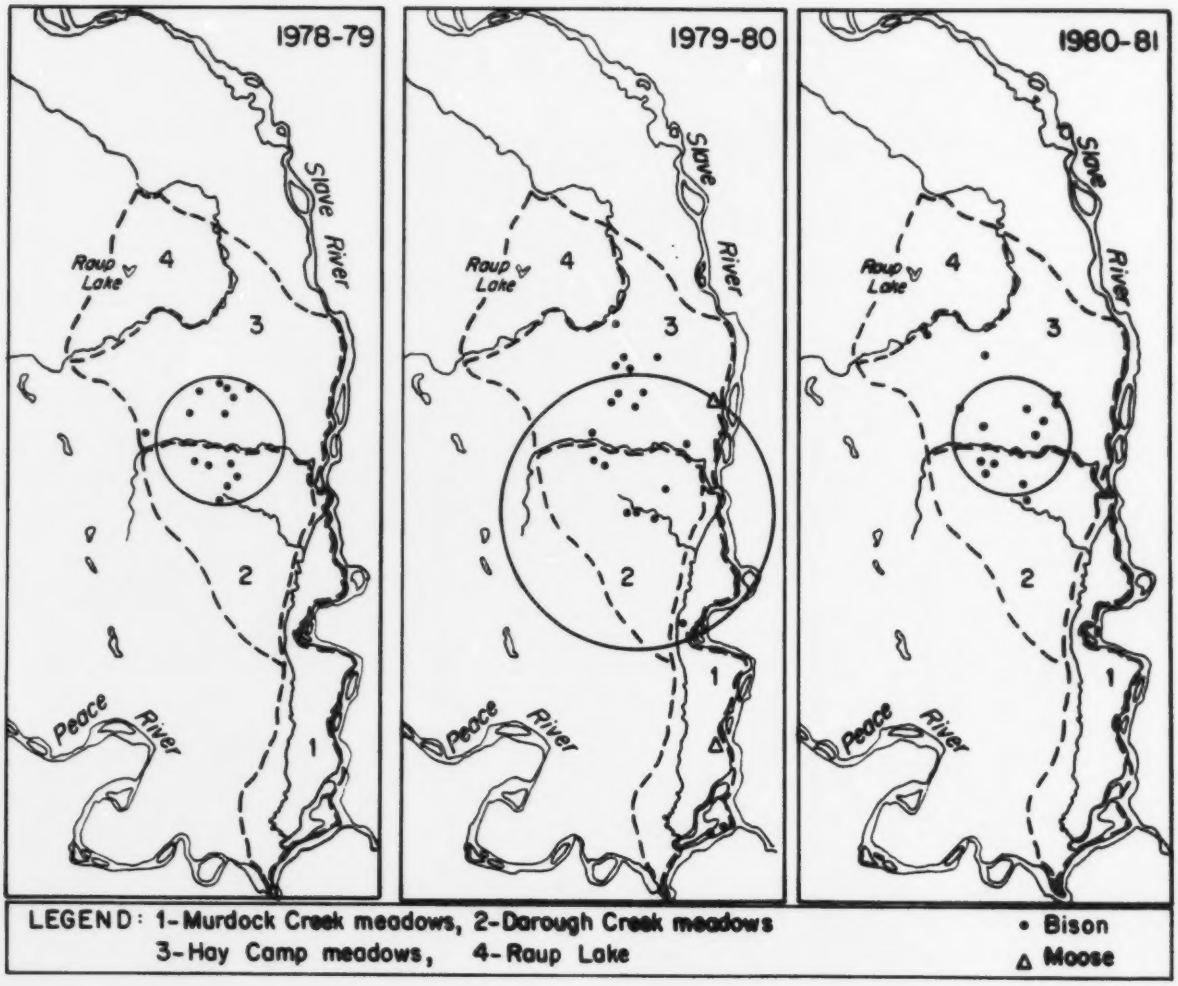


Figure 43. Location of kills and carcasses made and scavenged by the Hornaday River pack in winters 1978-79 to 1980-81, Wood Buffalo National Park. Circled area is pack's annual home range core.

Table 38. Relationship between bison abundance and distribution of bison kills made by the Hornaday River pack, winters 1978-79 to 1980-81, Wood Buffalo National Park.

Year	Total bison[1]	Total bison kills[2]	Percent of total bison, radiolocations, and total kills made by the Hornaday River pack											
			Raup Lake meadows			Hay Camp meadows			Darough Creek meadows			Murdock Creek meadows		
1978-79	2506	14	5.6	6.0	0.0	21.4	48.0	57.1	14.3	40.0	42.9	59.3	4.0	0.0
1979-80	3101	22	6.5	3.9	0.0	44.8	37.9	59.1	31.1	35.5	27.3	17.4	17.5	9.1
1980-81	3684	15	8.6	17.9	13.3	21.1	46.4	53.3	50.0	34.5	33.3	20.3	0.0	0.0
Total	9291	51	7.0	9.3	3.9	29.0	42.6	56.9	34.1	36.7	33.3	29.8	8.4	3.9

[1]See Appendix for a complete listing.
[2]Are carcasses consumed by the Hornaday River pack.

Table 39. Summary of wolf-bison encounters[1], winters 1977-78 to 1980-81; Wood Buffalo National Park.

Year	Watching prey	Approach prey and retreat	Prey attacked[2]	Prey killed	Total
1977-78	2	1	-	-	3
1978-79	5	1	-	-	6
1979-80	12	9	7	2	30
1980-81	10	7	6	1	24
Total	29	18	13	3	63

[1]Excludes multiple chase sequences observed on the same day.
[2]Charged and chased.

proportional to the available prey types (Table 40), although encounters and predation in 1978-79 were primarily directed toward bull groups and solitary animals (Oosenbrug and Carbyn 1982).

Hunting success of wolves preying on bison was determined in four ways: (1) As the number of successful attacks versus number of approaches and attacks observed, e.g. "testing" prey (Mech 1966; Peterson 1977); (2) As the number of successful versus unsuccessful chases, based on aerial observations of wolves and interpretation of tracks (Kolenosky 1972); (3) As the number of successful versus total encounters for various time periods that wolves were with bison prey; and (4) As the known number of prey killed versus the total number of encounters observed.

In the first instance, the wolves approached or attacked bison on 35 occasions (Table 39) and killed an animal on three, or 8.6% of these testing sequences. Secondly, wolves were successful on 32.5% of 86 chases observed from the air, or reconstructed from track evidence during the winters 1978-79 to 1980-81 (Table 41). There was no noticeable difference between 1979-80 and 1980-81, although the small number of observed chases in 1978-79 resulted in a high overall success rate for that year.

When the success rate was based on the wolves' prior presence with prey (Table 42), wolves succeeded in killing a bison out of a herd on 73% of the times they were with herds less than one day, and 100% when they were with herds for more than three days. On five occasions the wolves stayed with potential prey more than one day, e.g. they were seen on two consecutive days with the same herd, and they left without killing a bison. Four of these instances, however, occurred less than three days after the wolves had made a previous kill; the other resulted in a kill from the same

Table 40. Proportion of encounters and predation in relation to available prey types[1] for wolves north of the Peace River (Area I), winters 1978-79 to 1980-81.

	1978-79			1979-80			1980-81			1978-1981		
	Available prey types	Encounters	Kills found	Available prey types	Encounters	Kills found	Available prey types	Encounters	Kills found	Available prey types	Encounters	Kills found
Total observations	56	6	9	52	30	16	71	24	13	180	60	38
Bull-groups and solitary animals[2]	82.2	50.0	77.8	73.0	6.7	12.5	81.7	8.3	15.4	78.9	11.6	28.9
Herds	17.8	50.0	22.2	27.0	92.3	87.5	18.3	91.7	81.6	21.1	88.4	71.1

[1]Based on observations from midwinter annual total counts of Raup Lake, Hay Camp, Darough Creek, and Murdock Creek meadows.
[2]May include adult cows.

Table 41. Hunting success of wolves based on proportion of successful chases, as determined from aerial observations and track evidence, winters 1978-79 to 1980-81, Wood Buffalo National Park.

Year	Number of bison chases			Successful chases					
				Observed		Tracks		Total	
	Observed	Tracks	Total	Number	Percent	Number	Percent	Number	Percent
1978-79	1	7	8	0	0.0	7	100.0	7	87.5
1979-80	30	9	39	2	6.7	9	100.0	11	28.2
1980-81	15	24	39	1	6.7	9	37.5	10	25.6
1978-1981	46	40	86	3	6.5	25	62.5	28	32.5

Table 42. Hunting success of wolves in relation to previous encounters with potential prey, winters 1978-79 to 1980-81, Wood Buffalo National Park.

Killing success	Number of days observed with same herds[1]					
	<1	1-2	2-3	3-4	4+	Total
Unsuccessful	3	3	2	0	0	8
Successful	8	6	2	4	2	22
Total	11	9	4	4	2	30
Success rate (%)	73	67	50	100	100	73

	Number of days observed with same bull-groups, solitary bison, moose[1]					
	<1	1-2	2-3	3-4	4+	Total
Unsuccessful	5	0	-	-	-	5
Successful[2]	10	1	-	-	-	11
Total	15	1	-	-	-	16
Success rate (%)	67	100	-	-	-	69

[1]Includes all forms of encounters with prey (Table 40), followed by abandonment (unsuccessful) or killing of prey (successful).
[2]Includes one adult male bison and one adult female moose killed by members of the Salt River pack in 1979-80 and 1980-81.

herd two days later. On one other occasion the wolves spent less than one day with a herd before leaving unsuccessfully the next, then returned to the same herd a day later before killing a bison after three days with the herd.

When the two latter instances were included as successful encounters, the overall success rate for wolves preying on herds increased from 73 to 79%. The wolves overall success rate with bull groups, solitary bison, and moose (Table 42) was somewhat less (69%) than that for mixed herds, but the majority of these kills occurred within the first 24 hours of contact with the prey.

Finally, the relative success rate for the Hornaday River pack was higher in 1978-79, when the number of encounters per pack sighting was lowest, and the number of kills per encounter was highest (Table 43). This pattern of success for the Hornaday pack appeared to be related to predation on bull groups and solitary bison, which in every winter was highest for these prey types (Table 44).

An analysis of the Hornaday River pack's association with potential prey for which the outcome was observed (Table 45) indicated that in 1978-79, 1979-80 and 1980-81 the wolves were generally more successful in securing a kill if the kill was preceded by some form of previous encounter. Of the 52 encounters observed in the three winters, 18 (35%) resulted in kills within 24 hours, whereas 6% of non-encounters, i.e. where no previous associations were recorded, resulted in kills within a day (Table 45).

Table 43. Hunting success of the Hornaday River pack, based on number of kills found per observed encounter; winters 1978-79 to 1980-81, Wood Buffalo National Park.

Year	Number of daily observations[1]	Number of wolf-prey encounters[2]	Number of kills found	Number of encounters per observation	Number of kills per observed encounter
1978-79	47	4	10	0.085	2.50
1979-80	92	32	19	0.348	0.59
1980-81	77	24	13	0.312	0.54
1978-1981	216	60	42	0.277	0.70

[1]November to April inclusive.
[2]Excludes multiple chase sequences observed on the same day.

Table 44. Hunting success of the Hornaday River pack, based on number of kills found per observed encounter[1] for various prey types, winters 1978-79 to 1980-81, Wood Buffalo National Park.

Prey type	1978-79			1979-80			1980-81			1978-1981		
	Number of encounters	Number of kills	Number kills/ encounter	Number of encounters	Number of kills	Number kills/ encounter	Number of encounters	Number of kills	Number kills/ encounter	Number of encounters	Number of kills	Number kills/ encounter
Herds	2	2	1.0	28	14	0.5	22	11	0.5	52	27	0.5
Bull-groups and solitary bison[2]	2	7	3.5	2	2	1.0	2	2	1.0	6	11	1.8
Moose				2	1	0.5				2	1	0.5

[1]Excludes multiple chase sequences observed on the same day.
[2]May include adult cows.

Table 45. Hunting success of the Hornaday River pack, based on the pack's prior association with potential prey, winters 1978-79 to 1980-81; Wood Buffalo National Park.

Type of association	1978-79		1979-80		1980-81		1978-1981	
	Observations	Kills[3]	Observations	Kills[3]	Observations	Kills[3]	Observations	Kills[3]
Non-encounters	38	5	47	0	55	3	140	8
Encounters[1]	2	0	30	12	20	6	52	18
Unknown[2]	5	5	15	6	8	4	28	15
Total	45	10	92	18	83	13	220	41

[1]Excludes multiple chase sequences observed on the same day.
[2]Wolves not sighted.
[3]Kills made within 24 hours of observation on previous day.

Similarly, a summary of repeated attacks on bison herds (Table 46) showed that the Hornaday River pack exploited some herds on more than one occasion. Ten of the 12 repeated attacks on herds were successful; exceptions occurred on 14-15 February 1980 and 22-23 March 1980, when the wolves had already killed a yearling bison from the same herd a day earlier (13 February), and when the pack killed an adult cow out of an adjacent herd the next day (24 March). In two cases a minimum of three bison (all calves) were killed out of the same herd over the course of the winter (Table 46).

It was possible to document the Hornaday River pack's behaviour in relation to the number of days since its last known kill for 31, 73, and 71 observations in 1978-79, 1979-80 and 1980-81. Although in each winter the mean number of days since the last known kill was predictably greater for encounters than for non-encounters, there was no apparent pattern of increasing "active" interest in prey, i.e. approaching, attacking, or killing prey, with increased duration since the last kill (Fig. 44).

As expected, kills resulting from encounters became more certain as time from last kill was increased. Kill rates were greatest in 1980-81 and least in 1979-80. In all instances except one, medians were less than mean values (Fig. 44). In the latter case the majority of kills in 1978-79 tended to occur in the higher range of days since the last known kill.

Not much is known about hunting success of wolves. Mech (1966) and Peterson (1977) used the term "testing" where moose were approached or attacked, and reported that wolves killed 8% and 3%, respectively, of the prey they tested. Using these criteria, bison hunting success of 8.6% was similar to that proposed for moose by Mech (1966). This definition,

Table 46. Summary of repeated attacks[1] on bison herds by the Hornaday River pack, winters 1979-80 and 1980-81, Wood Buffalo National Park.

Herd number	Herd size	Date	Evidence of chase[2]	Chase distance (km)	After-kill flight distance (km)	Number of days with herd[3]	Number of previous kills from same herd
1	60	15/12/79	t	2.55	7.88	?	?
	60	17/12/79	t	4.94	7.11	2-3[4]	1
2	40	21/12/79	o	0.90	-	1	?
	40	22/12/79	t	3.99	8.01	1-2	?
3	65	13/02/80	t	0.20	3.15	1	?
	65	14/02/80	o	0.65	-	1-2	?
	65	15/02/80	o	0.92	-	2-3	?
4	90	20/02/80	t	0.10	6.48	1-2	?
	199	23/02/80	t	0.15	27.35	1	1
	120	02/03/80	o	0.07	13.18	?	2
5	23	10/03/80	t	0.10	11.51	4-5	?
	23	12/03/80	o	0.42	-	1-2	1
	43	14/03/80	t	0.30	9.53	3-4	1
	23	08/03/80	ot	16.16	-	2-3	?
	23	09/03/80	t	8.00	-	3-4	?
6	39	22/03/80	t	2.00	-	1	?
	47	23/03/80	t	2.50	-	1-2	?
7	90	08/02/81	o	0.18	-	1	?
	90	09/02/81	ot	0.52	-	1-2	?
	90	10/02/81	t	6.17	-	2-3	?
	90	14/02/81	t	0.20	-	1-2	?
	90	16/02/81	t	0.05	19.45	3-4	?
	90	06/03/81	t	1.00	-	1	1
	90	07/03/81	t	7.20	-	1-2	1
	90	09/03/81	t	4.30	81.45	3-4	1
8	300	25/02/81	t	3.20	0.80	1	?
	300	27/02/81	ot	1.62	-	1	1
	300	28/02/81	t	0.80	-	1-2	1
	230	28/02/81	t	6.10	-	1-2	1
	230	01/03/81	t	2.53	-	2-3	1
	230	02/03/81	t	0.76	-	3-4	1
	75	02/03/81	t	0.70	47.50	3-4	1
	22	18/03/81	o	6.25	-	?	2
	22	19/03/81	t	1.30	18.07	1-2[4]	2
9	25	23/03/81	t	3.40	-	1	?
	25	24/03/81	o	2.20	1.35	1-2	?
10	31	09/04/81	o	0.05	-	1	?
	26	14/04/81	t	0.80	?	3-4	?

[1]Charges and chases.
[2]Interpretation of chase based on: o = actual observations, t = track evidence, ot = observation and track evidence.
[3]Includes all forms of encounters with bison herds (Table 39) on consecutive days.
[4]Figures for the same herd are minimum values.

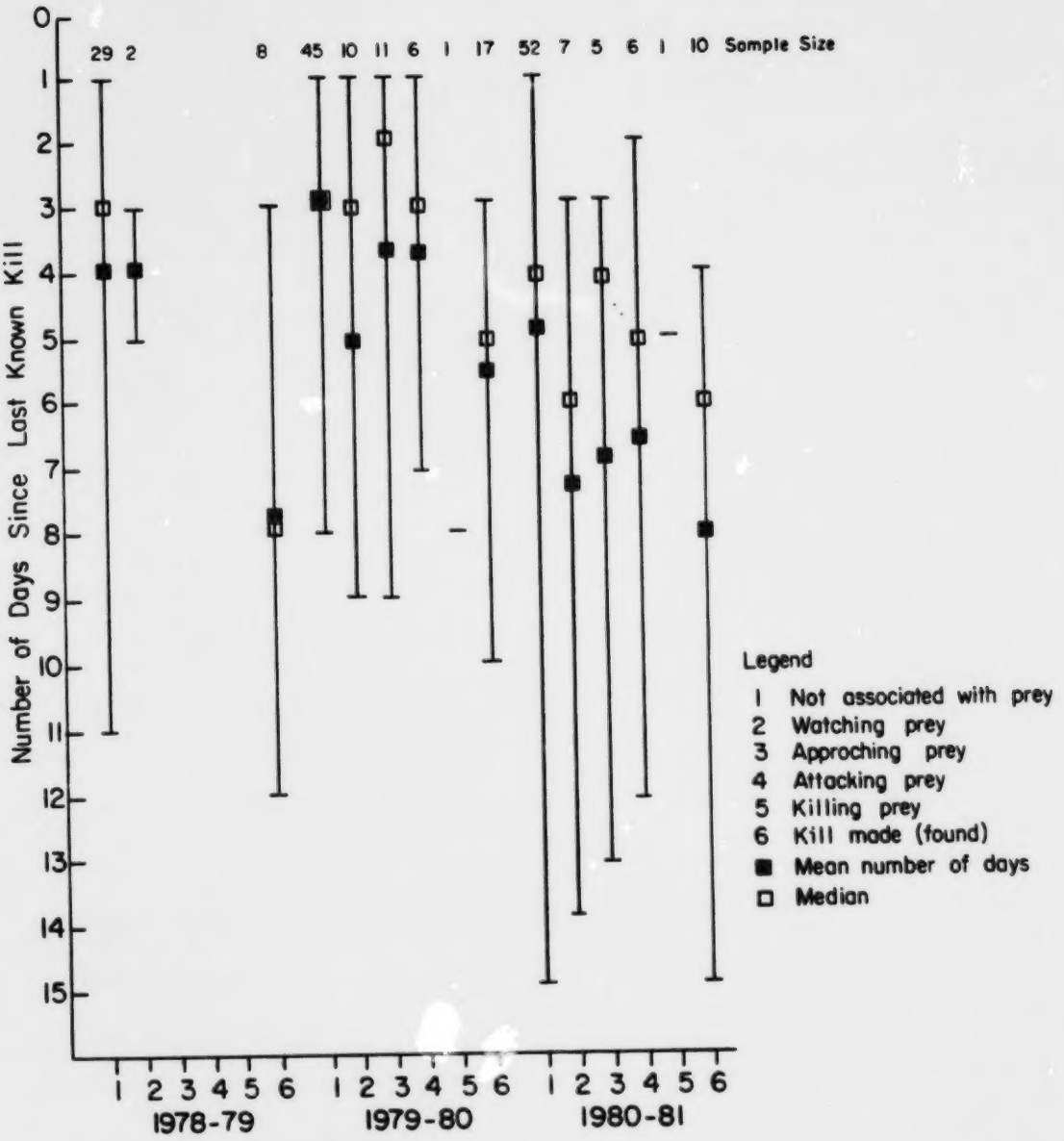


Figure 44. Pattern of wolf-prey behaviour in relation to number of days since last known kill; winters 1978-79, 1979-80, and 1980-81, Wood Buffalo National Park.

however, implied that the wolves only used approaches or attacks to test prey; we feel that wolves undoubtedly recognized vulnerable traits in prey that were not obvious to the aerial observers, and thus the observed hunting success may have been exaggerated.

In Ontario, Kolenosky (1972) reported that wolves succeeded on 25% of their hunts on deer in one winter, and 63% during another, but speculated that these rates may have been inflated because they were based entirely on track evidence usually originating from a kill site. In our study we used a combination of aerial observations and interpretation of tracks to document an overall success rate of 32.5% over the three winters, and noted that hunting success based on track evidence only, was much higher than that based on actual observations of chases.

The success rates quoted above are for wolves hunting solitary prey or relatively small groups, whereas wolves hunting bison preyed primarily on herds where more individuals may have been potentially vulnerable. It is conceivable that the hunting success rate of wolves attacking herds of prey may be somewhat higher than for wolves hunting solitary prey. Comparable information comes from another pack hunting species, the African hunting dog (Lycaon pictus) which preys primarily on herds. Hunting dogs apparently have a hunting success rate from about 34% (Van Lawick-Goodall 1971) to 85% (Estes and Goddard 1967). Hunting success for any species, however, depends ultimately on the vulnerability of the prey (i.e. age, condition), the efficiency of the hunting unit, as well as environmental conditions leading up to and at the time of the encounter.

Our data suggest that success rates increased with increased time spent with prey. If they did not kill quickly, wolves often left wounded

moose and began to search for other prey almost immediately (Peterson 1977). Wolves in Wood Buffalo National Park stayed with herds almost continuously for up to six days before making a kill, and their presence with herds may have been related to differences in distribution patterns of normally randomly dispersed solitary prey such as moose and deer, and highly mobile, clumped aggregations of bison. Kelsall (1968) reported that wolves were highly associated with caribou herds on their winter ranges, and often followed their tracks from one area to another.

Instances of wolves attacking the same herd on repeated occasions, often more than once successfully can also be explained in terms of wolf energetics and searching effort. Herds which were attacked more than once may have been easier targets than those which had first to be located, since the wolves knew where they were from tracks leading away from the previous pursuit or kill site. It is possible that the wolves purposely followed these herds in anticipation of isolating debilitated individuals, either from prior recognition or wounding. Fuller (1966) reported instances of wolves having previously wounded bison before eventually killing the animals at a later date. Alternatively, it could be advantageous for wolves to leave herds that are in a state of alert, and prey on animals not reacted by the presence of wolves (Carbyn 1975).

Most indicators of wolf hunting success suggested that the Hornaday River pack was most successful killing bison in 1978-79, although several complicating factors made the differences between this winter and the following winters less distinct. These included:

i) Most (7 of 10) of the kills in 1978-79 were of solitary bison (primarily bulls), for which chase success was based entirely on track

evidence. Interpretation of tracks in association with or without a kill was much easier for herds than solitary prey, therefore, in reality the number of successful chases involving solitary bison may have been less than observed.

ii) Analysis of encounters of wolves and bison where the outcome was determined indicated that, although most solitary bison kills occurred within 24 hours of first recorded contact of wolves and prey, killing success for solitary bison (mostly 1978-79) was actually somewhat less than for herds (mostly 1979-80 and 1980-81).

iii) The disproportionate number of kills of solitary bison (mostly bulls) versus actual observations of wolf-prey encounters, most likely indicated that solitary bison were indeed killed more quickly than those associated with herds. However, since chases of solitary bison were difficult to discern, and since on only one occasion was a solitary bison (bull) actually observed being killed by a pack of wolves (18 February 1980), it is possible (though doubtful) that some of the solitary bison kills were bison that died prior to contact with wolves.

iv) Although the availability of solitary bison over the composite Hornaday River pack's winter range was similar in every year, predation on solitary bison and association between the pack and all bison was highest in 1978-79, suggesting that certain circumstances in 1978-79 existed which facilitated association with and predation on solitary bison. Snow conditions in late winter 1978-79 were more extreme than usual, and related bison condition was poor (Kingsley 1982).

Shifts in wolf-prey encounters and predation from primarily solitary bison in 1978-79 to primarily herds in 1979-80 and 1980-81 appear to be

best explained by changes in vulnerability of available prey types during the last two winters. We believe that solitary bulls were in relatively better condition in 1979-80 and 1980-81 than calves in herds, the latter whose condition may have been the result of *in utero* stress during 1978-79. Wolves likely concentrated on herds once the searching effort for and chance of an unsuccessful encounter with solitary bison exceeded the energetics of time spent with, and chases of herds.

b. Patterns of wolf attacks

Conclusions about hunting strategies of wolves preying on bison in winter in Wood Buffalo National Park were based on 143 observations of wolf-bison encounters, track evidence, and reported wolf-killed bison from winters 1970-71 and 1980-81. We used a progression of events similar to that proposed by Mech (1970) and Carbyn *et al*. (1980) to describe wolf attacks on bison herds. This progression included five phases, each linked by the wolves' behaviour and bison's counter behaviour. These were: (1) Recognition phase, (2) Approach phase, (3) Initial charge phase, (4) Sustained chase phase, and (5) Contact phase. Encounters between wolves and solitary bison followed a similar pattern, but usually did not involve a sustained chase. A description and discussion of each phase in given below.

i) Recognition phase

This was considered the stage at which the wolves first became aware of the prey, and responded by stopping and altering their route of travel. In most cases (7 of 11) wolves appeared to recognize potential prey by sight at distances of about 100 to 500 m. These initial encounters were recorded in open meadows, thus, perception of the prey at other times

may have occurred from much greater distances. In one of the instances the lead wolves hesitated, resulting in the pack bunching with considerable interaction between members. The lead animals stared intently toward the herd for nearly a minute before beginning an approach.

Mech (1966) reported that wolves hunting moose on Isle Royale located their prey primarily by smell. Wolves in this study (4 of 11 times) appeared to be following bison tracks and may have used a combination of sight and smell to locate potential prey. It is conceivable that wolves in Wood Buffalo National Park may depend on sight to a greater degree than wolves on Isle Royale, as the winter terrain of bison is more open than that of moose on Isle Royale.

Bison initially reacted little to the presence of wolves, although their reported sense of smell and ability to distinguish movement (Fuller 1960) undoubtedly enabled them to locate wolves readily. Earlier authors (Goodwin 1935; Soper 1941; Fuller 1960) noted a general indifference by bison to wolves in close proximity, and this behaviour was also recorded in summer at Lake One (Oosenbrug et al. 1980b, 1981; Carbyn et al. 1981).

ii) Approach phase

Unlike summer, when wolves at times hunted singly (Oosenbrug et al. 1980b:32), wolves in winter rarely "stalked" bison (1 of 23 observations), as reported by Mech (1970) for wolves preying on moose. Rather they walked deliberately toward bison, making no attempt to use cover, or to approach the prey from downwind.

Herds normally reacted by bunching while facing the approaching wolves (10 of 23 observations; see also Fuller 1960). Sometimes, however, they faced the wolves in an open formation, behaved aggressively toward the

wolves, hesitated to stand, or outright ran (2, 3, 3 and 4 cases). If the herd stood and faced the wolves (14 observations), the wolves retreated, laid down nearby, or moved gradually away from the herd.

iii) Initial charge phase

If on the approach bison were hesitant to stand (i.e. seemed uncertain, or ran) the wolves charged at the herd (7 observations), and the herd would turn and run with the wolves in pursuit. In some cases (4) wolves charged a herd without a prior approach, but these always occurred with herds that had previously been chased; in two instances the wolves charged a still-standing herd.

It was often difficult to tell whether the bison or wolves initiated flight, however, Mech (1975b) implied that the prey initiated flight and in turn triggered a chase response in wolves. This appeared to be the case with bison and wolves. Bison were judged to be the initiator of chases in 27 of 30 observations. Peterson (1977) concluded that vulnerable moose invariably ran when approached by wolves, and it is conceivable that potentially vulnerable animals in a herd of bison would tend to run, taking the rest of the herd with them, and thus eliciting a chase.

iv) Sustained chase phase

In all cases (n = 30), once a herd began to run the wolves gave chase. Most chases were full-out pursuits (26 of 42 cases), with the remainder consisting of following (1 case) and a combination of pursuit and following (15). Chase distances of full-out pursuit did not exceed 500 m (mean distance 150 m, median 80 m), but total distance traveled by wolves and their potential prey often took place intermittently over several days and varied from 0.2 to 24.3 km (Table 46). Although full-out pursuits were

often short, wolves chasing other ungulates, including moose (Mech 1966), caribou (Murie 1944; Crisler 1956), and deer (Dunne 1939; Kolenosky 1972; Mech and Korb 1978) appeared to pursue and follow their prey over relatively long distances, largely in order to isolate vulnerable individuals. Mean distances of successful chases in our study were slightly greater in 1979-80 than in 1980-81 (Table 47), but were lowest in 1978-79 both for herds and solitary bison. Only two chases were less than 0.01 km; both occurred in 1978-79. The longest successful, and unsuccessful chase (4.9 and 16.0 km) occurred in 1979-80.

The speed at which wolves chased bison varied somewhat with the speed at which the bison were running, and the prevailing snow conditions. On every occasion and under all circumstances, the wolves appeared to have no trouble catching up to the fleeing bison. For example, on 21 December 1979 the Hornaday River pack caught up to within 1200 m to a herd of bison which had a 500 m lead when the chase started. Stenlund (1955) reported that wolves were capable of running at speeds of 55-65 kph over a distance of 6.5 km. We believe that bison probably did not exceed 40 kph over the most favourable winter terrain, and the speed with which wolves caught up to the bison is reflected in the relatively short chase sequences of full-out pursuit.

Wolves pursuing caribou were reported to refuse chases into deep, soft snow (Kelsall 1968) when depths exceeded 40 cm and density was less than 0.21. Caribou apparently were able to outrun wolves under these circumstances (Nasimovich 1955). This type of situation was also reported for wolves and moose on Isle Royale (Mech 1966).

Table 47. Mean chase distances by the Hornaday River pack of bison, based on aerial observations and track evidence; winters 1978-79 to 1980-81, Wood Buffalo National Park.

Year	Mean chase distance (km)				
	Successful chases[1]			Unsuccessful chases[1]	
	Full-out pursuit of herds	Pursuit of solitary bison	Pursuit and follow herds[2]	Full-out pursuit of herds	Pursuit and follow herds[2]
1978-79	0.08 (6)[3]	0.06 (6)[3]			
1979-80	0.15 (5)	0.26 (2)	3.25 (4)	0.14 (21)	4.59 (8)
1980-81	0.11 (3)	0.18 (1)	2.50 (7)	0.16 (14)	3.04 (13)
1978-1981	0.11 (14)	0.12 (9)	2.77 (11)	0.15 (35)	3.47 (21)

[1]Sample size (observations) given in brackets.
[2]Includes total distances traveled by wolves with bison.
[3]Eleven of 12 chases determined from ground examination of track evidence.

In this study there was no apparent pattern of chase distances related to snow depth, either within or between winters (Table 48). Consideration of other factors such as herd size, pack experience and motivation (e.g. chase length related to days since last kill), and herd "psychology" (e.g. herds in late winter may have been more reactive to wolf attacks), resulted in such small sample sizes of observations that interpretation of chase lengths became meaningless.

An examination of the habitat distribution for bison locations, chase sequences, and wolf-killed bison in Area I (Fig. 45) showed that:

(1) prairie-meadow was the habitat most commonly occupied by herds, bull groups, and solitary bison, and

(2) chases somewhat, and kills more so, occurred less than expected in prairie-meadow, expectedly in deciduous shrub, and greater than expected in mixed forest habitats.

It was not possible to determine whether the bison selected the chase route or whether the the wolves deliberately drove the bison into the trees. It is conceivable that obstructions (i.e. windfalls, undergrowth) hindered the smaller bison during a chase through the forest, resulting in these animals falling behind or separating from the herd; 41% of all calf and yearling kills (n = 22) occurred in the forest. Similar figures were recorded for adult bulls (50%) and cows (38%), although these may have included unsuccessful attempts to ward off wolves. Fuller (1960) reported that wounded bison often sought refuge from wolves in the trees; in two instances we noted adult bison behave in this manner.

In most chases (67 of 71 observations) the wolves concentrated on the bison in the rear of the herd, attempting to make contact with slower

Table 48. Mean chase distances by the Hornaday River pack of various bison groups, based on aerial observations and track evidence, winters 1978-79 to 1980-81, Wood Buffalo National Park.

	Mean snow-depth[3] (cm)	Full-out pursuit (m)[1] Herd size					Pursuit and follow (km)[1] Herd size				
		0-10	11-30	31-100	100+	Total	0-10	11-30	31-100	100+	Total
Early winter[2]											
1978-79	15										
1979-80	15			128(4)		128(4)					
1980-81	21		150(1)			150(1)			3.7(3)		3.7(3)
Mean	17		150(1)	128(4)		132(5)			3.7(3)		3.7(3)
Midwinter[2]											
1978-79	34	77(3)		50(1)		70(4)					
1979-80	42	260(2)		123(8)	150(1)	150(11)					
1980-81	34	175(5)		143(11)	75(2)	136(14)			6.3(2)	5.1(1)	5.7(4)
Mean	37	154(6)		130(2)	100(3)	132(29)			6.3(2)	5.1(1)	5.7(4)
Late winter[2]											
1978-79	31	30(2)		105(3)		75(5)					
1979-80	23		127(10)	275(2)	70(1)	145(13)		6.3(4)	2.4(4)		4.3(8)
1980-81	28		275(2)	120(1)		223(3)		1.6(7)	3.3(4)	1.1(3)	2.0(14)
Mean	27	30(2)	152(12)	181(6)	70(1)	145(21)		3.3(11)	2.8(8)	1.1(3)	2.8(22)
Total		123(8)	152(13)	140(30)	93(4)			3.3(11)	3.6(13)	2.7(5)	

[1]Successful and unsuccessful chases combined; sample size (observations) in brackets.
[2]Early winter = November-December; midwinter = January-February; late winter = March-April.
[3]Cumulative mean determined from four mid- and end-month measurements at Fort Smith airport.

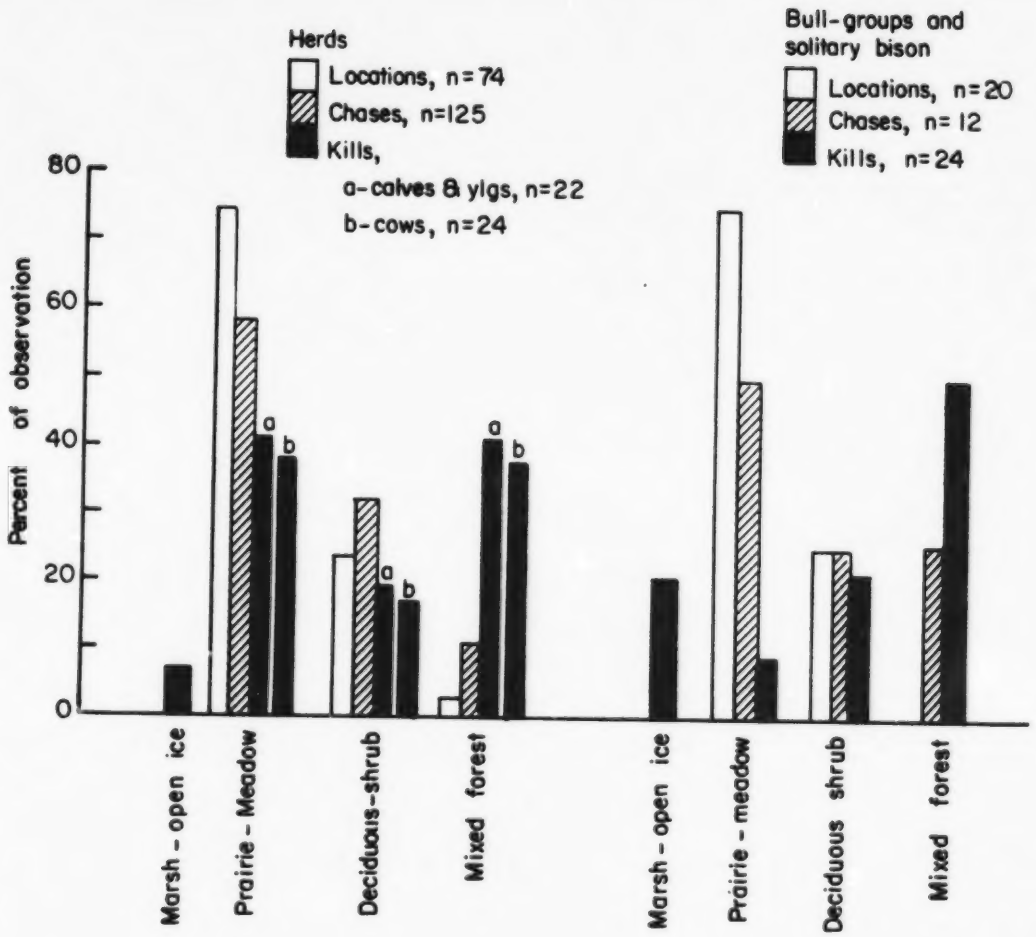


Figure 45. Habitat distribution for bison locations, chase sequences, and wolf-killed bison in areas north of the Peace River (Area I), Wood Buffalo National Park; winters 1977-78 to 1980-81 combined.

individuals, breaking their stride, and thus separating them from the rest of the herd. However, on two occasions when individual bison stopped to face the wolves and defended themselves, the wolves continued after the fleeing herd.

Kelsall (1968) described three methods by which wolves successfully hunted caribou year-round: (1) stealth and ambush, (2) relay running, and (3) herd induced hindrance. No evidence of wolves ambushing bison was recorded in this study, although wolves hunting bison in winter used what possibly can be interpreted as relay running.

Relay running involved a chase with wolves strung out behind the herd, with one or two wolves leading the attack, the others following behind, taking advantage of the turns of the chase to save time, energy, and to close in on the trailing bison. An example of this occurred on 15 February 1980, when a herd of 53 bison was pursued by 11 wolves during four chase sequences. The incidence is summarized below:

"At 0945, 15 February 1980, the Hornaday River pack was resting 100 m east of a herd of 53 bison, including one calf. At 0950 the pack began a slow, but deliberate approach from behind some willows. As soon as they were out in the open, 50 m from the herd, the bison began to run, 42 running north toward a herd of 12, with 11 (mainly bulls) left behind as the herd was separated. The wolves ran past the standing group of 11, and ran full-out (2-3 abreast, with the rest of the wolves trailing behind) after the moving herd. Within 100 m from the start of the chase, a single cow stopped and turned around, and the wolves ran right past it as it returned to the remaining 11 bison. Another 100 m and two bulls were caught behind and away from the fleeing herd. One turned around and the

wolves ran by; the other was also passed by, but it eventually caught up with the herd as it turned to face the wolves after a distance of about 350 m. From 0955 to 1010 three more chase sequences of 100, 70, and 120 m occurred, with the herd winding through the meadow around willow shrubs, and the trailing wolves cutting corners in order to keep up with the lead wolves. Although no visible contact was made by the wolves, each chase sequence terminated when the lead wolves caught up with the trailing bison, and the entire herd turned. The herd eventually joined the group of 12 and milled around as the wolves lay down 50 m to the south."

Under certain circumstances, such as when attacking large herds of 100 or more bison, or when pursued bison were hesitant to enter the trees, the wolves would momentarily come in close contact with bison whose escape route was blocked by those farther away from the wolves. Unlike caribou, any one of which would be vulnerable to such a confrontation (Kelsall 1968), bison generally were not killed under these circumstances. Exceptions were calves, which seemed to be particularly predisposed to wolf attacks. An example of this occurred on 2 March 1980, when 10 wolves charged a herd of about 120 bison at the edge of a willow stand. At 1300, the Hornaday River pack was resting at the edge of some willows 100 m west of the herd. At 1305 several cows at the front of the herd began to move away from the wolves, and almost immediately the rest of the herd followed their lead and was also moving. The wolves were up quickly and ran toward the herd, one wolf in front at full speed. The bison broke into a run, stampeding into the willows, with the wolves catching up in seconds.

Between 1306 and 1307 there seemed to be general confusion among the bison, as the herd seemed to be unable to decide in which direction to

flee. A this time five or six wolves made contact with a calf, surrounded it and downed it almost immediately. The calf continued to struggle but within two minutes had been overwhelmed by the wolves and dragged down. The rest of the herd continued to run to the north, with the remaining five or six wolves among them. A brief skirmish followed as one of the bison became separated and was attacked by three wolves. However, it was quickly let go and eventually caught up with the escaping herd.

From 1310 to 1315 the calf was being fed upon by at least six wolves, several others headed back to the carcass and were caught between a group of eight bison which were moving north to catch up to the herd. The wolves were forced to jump off the trail into some deep snow, and one bison nearly pinned one of the wolves to the ground with its head.

v) Contact phase

If the wolves were able to isolate a perceived vulnerable individual from a herd, or had surrounded a similar solitary animal, they generally attacked the rear of the bison in an attempt to wound and incapacitate the hind leg muscles (Table 49). Depending on the reaction of the bison, the wolves would continue to tear at the hindquarters as the bison circled rapidly to ward off the attack with its head, or would hold on to the bison's hind legs as it attempted to escape. Calves were held similarly while other members of the pack tried to knock it off its feet.

In three instances where contact was made, the bison did not escape and were actually observed being killed. On two other occasions contact was suspected but not confirmed, and the bison managed to rejoin the herd. An example of a bison being separated from a herd and unable to catch up with it again occurred on 24 March 1981, when eight wolves were observed

Table 49. Summary of wounding in bison killed by wolves in Wood Buffalo National Park, winters 1978-79 to 1980-81.

Date	Group size	Number of wolves	Estimated age of prey[1] (yr)	Sex	Primary areas of wounding
19/01/79	3-5	14	6	Bull	Rump, anus, nose (?)
26/01/79	35	7	10	Cow	Rump, shoulder
30/03/79	70	6	1	Cow	Hind legs, flanks
21/04/79	?	6	Adult	Cow	Anus, shoulder
10/01/80	?	6	Adult	Cow	Flanks, abdomen
18/02/80	1	7	7	Bull	Flanks, rump
02/03/80	120	10	1	Bull	Rump, shoulder
16/02/81	98	8	8	Cow	Rump, flanks
24/03/81	25	8	12	Cow	Flanks, anal area

[1]Determine by cross section of incisor and examination of horn annuli.

Table 50. Bison herd response to wolf testing[1] in relation to prior association and number of observed chase sequences by the Hornaday River pack in winters 1979-80 and 1980-81, Wood Buffalo National Park.

	Number of consecutive days wolves observed with same herd[2]					Number of previous chase sequences observed on the same day							
Stand	<1	1-2	2-3	3-4	Total	0	1	2	3	4	5	6	Total
Herd size													
10-30	4	2	1	1	8	8	-	-	-	-	-	-	8
30-100	0	2	0	0	2	2	-	-	-	-	-	-	2
100+	1	0	0	1	2	2	-	-	-	-	-	-	2
Total	5	4	1	2	12	12	-	-	-	-	-	-	12
Run													
Herd size													
10-30	2	2	2	-	6	4	3	3	2	1	1	1	15
30-100	2	1	1	-	4	4	4	4	2	0	0	0	14
100+	1	0	1	-	2	2	1	0	0	0	0	0	3
Total	5	3	4	-	12	10	8	7	4	1	1	1	32

[1]Approaching or charging bison.
[2]Includes all forms of wolf-bison encounters (Table 39).

chasing a herd of 25 bison in the northwest corner of the Darough Creek meadows and the sequence was as follows:

"At 0940 the Hornaday River pack was running approximately 1 km behind the main portion of a herd of 25 bison. The wolves were running in single file over a distance of 500 m, led by one wolf which was at least 100 m ahead of the others. Two groups of bison, one of 7, and one of 2 animals, had stopped running and were standing in the line of the chase. At 0942 the lead wolf reached the second group of bison, after having run past the first group of seven bulls. The two bison put their heads down and charged the wolf as it ran past them, and they chased it for 10 m as the wolf continued after the group of 16 that was running southeast. Two other wolves ran by the two bison (both cows) at 0943, but the remainder of the pack began to harass these two as they reached them by 0944. As soon as the first three wolves realized the rest of the pack was attacking the two bison, they ran back and joined in the attack. By 0945 all the wolves were circling, lunging, and snapping at the two bison, but one of these managed to run from the wolves, whereupon the pack concentrated its attack on the remaining bison. Between 0945 and 0955 the wolves were pressing all around the cow, trying to get at it from the rear, biting the rump and anal area. The cow tried to ward off the attack with its head, but the wolves continued to circle to the rear with the result that the cow was continually turning in circles. In the meantime the cow tried to run after the herd, which at this point was at least 1 km away, and still moving into the open meadows. Trail conditions allowing, the wolves would grab at and tear the cow's flanks, and where the trail was narrow they would follow in

file until the trail widened and several wolves would grab at the cow's hind end. During much of the pursuit one of the wolves ran in front of the bison, possibly to distract it (Fig. 46) or to attempt to grab at the muzzle. At 0955 the bison was visibly tiring as it struggled through the snow with several wolves hanging on its hindquarters. The harassment and wounding had taken place over 750 m from the first confrontation to where the cow had dragged itself into the trees to face the wolves. By 1000 both wolves and bison were in the trees. The cow had stopped running but the wolves continued the attack, coming in from behind and wounding the bison. The two light coloured wolves were covered with blood; several wolves were resting as the others continued to press. At 1005 the bison was standing in the trees, its hindquarters shaking. As it fell over once, the wolves closed in on it immediately and began to tear at its abdomen. The cow managed to get up and dragged itself 10 m with several wolves holding on to its hindquarters. At 1007 the bison was still on its feet, standing and facing the wolves with its tail up. Some of the wolves were resting nearby, and the bison lunged at several standing close; the wolves stepped back. At 1015 the bison was down; although its head was still up, the wolves were tearing at its abdomen. By 1030 the wolves were feeding, the bison's head rose occasionally, but it was close to death. The herd of 16 had stopped 800 m to the southeast at the edge of the open meadows and some were beginning to graze."

Examination of the carcass the next day showed that this was a mature cow. Damage was almost entirely restricted to the hindquarters. The body was intact except for holes in the flanks and anal area; all the

Figure 46. Hornaday River pack pursuing and attacking an adult female bison, 24 March 1981; Wood Buffalo National Park.

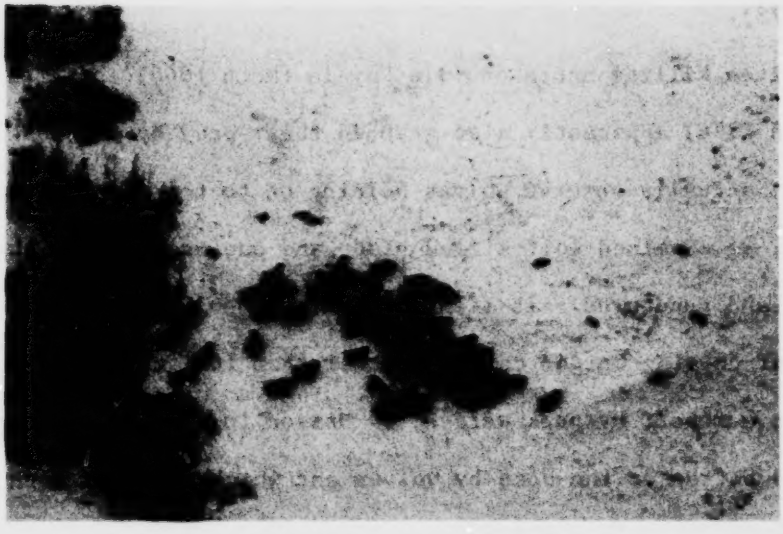


Figure 47. Typical defense formation of a bison herd facing approach by the Hornaday River pack (8 wolves?), 14 February 1980; Wood Buffalo National Park.

internal organs had been removed from the body cavity and consumed. Evidence of pregnancy included a portion of a fetal hoof.

Historical information on wolves killing bison is scant. Garretson (1938:73) described a graphic incident related to him of wolves severely wounding an adult bull, although the accuracy of this seemed somewhat suspect. During his studies of bison in Wood Buffalo National Park in the 1950s, Fuller (1960, 1966) observed several wolf attacks and examined a number of bison wounded or killed by wolves. He concluded that wolves appeared to single out one animal in a herd, which might be the subject of repeated attacks if the first attack was unsuccessful. Wounding normally occurred in the thighs, shoulders (calves), and flanks. Wounding in a similar sized ungulate (moose) resembled our observations (Table 49), in that moose killed by wolves invariably were severely wounded in the rump or upper portions of the hind legs (Burkholder 1959; Mech 1966; Buskirk and Gipson 1978).

Wolves killing moose on Isle Royale (Mech 1966) and Alaska (Buskirk and Gipson 1978) apparently also grabbed their prey by the nose. Although we did not actually observe wolves holding on to the nose of bison during an attack, we examined wolf-killed bison and one moose where the nose had been torn and punctured. It is not known whether nose damage may have been a result of chewing on the carcass rather than inflicted during an attack. Aside from a report by park warden, G. Masson in 1973 of a bison which had been badly bitten on the nose by wolves and which was shot because of its severe wounds, wolf-killed bison were characterized by lack of facial wounds. This might be expected, as the bison's primary means of defense in winter is the use of its head and horns to ward off attacking wolves.

Compared to the long, fleshy nose of a moose, a bison's nose is unobstrusive and surrounded by massive bone and thick and abundant facial hair. Evidence of this study suggested that under most circumstances wolves avoided frontal attacks and concentrated on the posterior region. Furthermore, frontal and side attacks could be less successful because of the thick coat of woolly hair.

In conjunction with posterior attacks, we noted that the tail of wolf-killed bison was often missing (Carbyn et al. 1981). During both summer and winter we frequently observed bison with missing tails, and suspected that wolves were responsible.

The following account describes the killing of an adult male bison where wolves concentrated on the posterior region of the bison, and were observed hanging onto it tail during the attack.

"On 18 February 1980, we spotted a pack of seven wolves resting on the bank of the Salt River. We returned to Fort Smith for a helicopter to capture members of the pack. At 1310 we located the pack 1.2 km east of its original position in the process of attacking a solitary bull. From the trampled areas, it appeared the bull had probably been under attack since 1300 and had fought off the wolves at four locations prior to our arrival.

Between 1310 and 1330 the wolves attempted to get at the rear of the bull, while it kept spinning around to face and fend off the wolves with its head. The bull broke into a run several times with some of the wolves hanging on to its flanks, rump and tail. It ran into some willows on three occasions and was unable to partially shake the intensive attack of the wolves. Attacks were almost continuous, with several of the wolves darting

in from the rear and grabbing the bison's hindquarters, forcing it to turn, at times dragging two or three wolves with it. The wolves would break from the attack for 15-30 second intervals, and the bison faced them with its tail up.

Attacks from the rear continued from 1330 to 1350. At one time we noticed one wolf holding on to the bison's tail for about 10 seconds as the bison spun around, dragging the wolf with it through the willows. The bison appeared to be severely wounded and visibly tiring, although it did not go down at any time. At 1350 all animals were panting heavily; several of the wolves lay down while the bison stood facing the rest in a dense willow stand. Some of the wolves were covered with blood around the muzzle and neck, and the bison seemed to be bleeding profusely from the rump and flanks.

By 1400 we assumed the bull was mortally wounded, and we proceeded to capture three members of the pack. The wolves were hesitant to leave the bison, but were manoeuvered into the open and darted within 30 minutes. The wolves did not attack the bison again, probably due to our disturbance, but it died the next day and the wolves fed on the carcass from 19-24 February.

Our observations of wolf attacks on bull groups and solitary bison are few. Fuller (1966) speculated that mature and healthy bison, whether in herds, small groups, or as solitary individuals, were virtually immune to wolf predation. We witnessed from the air two successful attacks by packs on apparently healthy, mature bison. One of these was on a solitary bull, and in the other instance on a cow which had not kept up with a fleeing herd. Examination of each carcass did not reveal any

obvious physical infirmities, although the cow had necrosis of the jaw and was pregnant.

Single wolves may also be capable of killing solitary bison under circumstances similar to those described for a single wolf killing a lone bull muskox (Ovibos moschatus) (Gray 1970). In one case we located a single wolf feeding on a fresh carcass of an adult bull bison, but could not determine whether it had been killed or had died prior to being found by the wolf. A local trapper (D. Dragon, pers. comm.). reported an incident of a single wolf following the tracks of a single bison for over 20 km along a roadway before he found the wolf feeding on the fresh carcass of an adult bull. Since the condition of neither victim was known, it is conceivable that the wolves did not actually kill the bison, although in the latter case at least, the wolf may have hastened the bison's death.

Although we documented a variety of physical infirmities in bison killed by wolves, and there may have been other debilitating factors such as tuberculosis (Fuller 1966) which we were unable to diagnose. We believed that under the "right circumstances" all bison, whether healthy or not, were vulnerable to wolf attacks in winter. These circumstances included the following:

i) Snow conditions

In winter, bison due to their relatively short legs, have difficulty manoeuvering in snow depths exceeding 65 cm (Van Camp 1975), and unlike in summer (Oosenbrug et al. 1980b:31) cannot effectively use their feet to defend themselves. This situation is aggravated when snow crusts are strong enough to support wolves, but not bison. Late winter snow conditions, combined with poor condition of solitary adult bison, may

explain the large proportion of adults killed by wolves during the winter of 1978-79 (Oosenbrug and Carbyn 1982).

ii) State of hunger in wolves

We suspect that wolves which approached and retreated from solitary adult bison were either not hungry, and/or felt the bison was too difficult a target. The wolves' subtle recognition of a potential victim no doubt escaped our detection. A wolf response to the detection of a crippled bison in summer 1980 provided evidence that wolves can quickly perceive debilitating conditions in their prey (Carbyn et al. 1981), but we suggest that hunger may override the prudence of not attacking a "healthy" bison, as we believe it did with the Salt River pack killing an adult bull in 1980.

c. Bison defense mechanisms

On being approached by wolves, bison in most instances faced toward the predator (44 of 58 observations), whether the bison were in a group, or alone. Herd formation tightened quickly depending on the manner in which the wolves approached the herd. It appeared that cows with calves moved toward the centre or portion of the herd farthest away from the wolves although this factor was not quantified. Normally if the herd stood the wolves were unwilling to attack.

Interactions along the periphery of the herd (Fig. 47) involved primarily bulls, but at times cows without calves also appeared aggressive toward the wolves. These peripheral animals, by virtue of their proximity to the wolves, appeared to be risking their own safety in defending the herd, although they retreated if they perceived themselves isolated from the other bison. Summer observations of herds facing wolves were similar

(Oosenbrug et al. 1980b, 1981; Carbyn et al. 1981) in that bulls appeared to be the bison which primarily fended off approaches by wolves.

An analysis of bison herd response to attacks by the Hornaday River pack in relation to prior association with that pack, and the number of previous chase sequences observed on the same day (flight), indicated that although the bison's reaction to run did not appear to increase with longer time spent with wolves, this behaviour was greatly increased if herds had been chased before (Table 50). Herds stood on 55% (12 of 22 observations) of the initial approaches or charges by wolves, but ran on all subsequent charges. Small herds (10-30 bison) stood on 57% (8 of 14 observations) of all wolf attacks, and 67% (8 of 12 observations) of initial approaches or charges by wolves on the same day, compared to 40% (4 of 10 observations) and 40% (4 of 10 observations) respectively for all other herd sizes. Similar interpretation of distances fled by herds after kills made by the Hornaday River pack (Table 46) suggested that bison were sensitive to a combination of time spent with wolves and the number of kills made previously from the same herd.

If in fact a standing herd is the strongest line of defense, why then do bison run? We can only speculate that a psychological strain of some sort to some of the bison resulted from the wolves' presence, which caused an escape reaction and breakdown of herd formation. Curio (1976) has argued that this behaviour of flight may be a manifestation of individual selection overriding kin selection, in that although the chances of losing a member from a running herd are relatively great, the chances of death to any one individual in the herd are relatively small. Taking this one step further, we could say that the chances of being killed for any one

fleeing bison decrease with increasing herd size, and is greatest for solitary animals. This theory may explain observations of the tendency of solitary moose to stand and ward off wolves, while those which run are invariably killed (Mech 1966, Peterson 1977).

If we conclude that bison separated from herds, or solitary bison, when attacked by wolves have a slim chance of survival, why then do not all bison exist in herds which minimize the chances of predation on each individual? The answer probably lies partly in the social organization of bison, whereby groups of "bachelor males" (Meagher 1973; Fuller 1960) spend a considerable part of the year away from the cow-calf herds. It is conceivable that small, scattered groups or solitary bison may have developed an anti-predator strategy similar to other solitary ungulates whose main defence possibly is non-detection. Individuals in herds may be less vulnerable, yet they are much more readily detectable, and may be subject to multiple attacks.

Herds could well be responding to predation pressure by emigrating out of areas of extreme wolf predation, and by annually altering their patterns of distribution. During the winter 1980-81 several cow-calf herds fled long distances in response to repeated harassment from the Hornaday River pack. These bison traveled into areas of marginal winter habitat, but outside of the normal winter range of the Hornaday River pack (Table 46). It is possible that the pressure of predation from this particular pack was such that it prompted these herds to travel into inferior habitat and remain for a time undetected by other wolves. Although bison in our study area normally occupied traditional wintering areas, notable exceptions occurred in 1978-79 and 1980-81 when winter bison

distribution was shifted to alternate ranges. These annual shifts in winter range have also been documented previously (Tempany and Cooper 1976; Collingwood and Millette 1977), and their unpredictable nature may be an adaptive form of predator avoidance behaviour.

3. Food habits of wolves

a. Prey selection

Of the 130 bison carcasses examined in Wood Buffalo National Park from winters 1971-72 to 1980-81 which were suspected or confirmed kills, 39 were adult males, 41 were adult females, 9 were adults of unspecified sex, 10 were yearlings, and 31 were calves. Age and sex classes are presented in Appendix 7.

Ages of bison killed by wolves from 1971 to 1981 (Fig. 48) compared with the estimated winter age structure of the population (Table 51) showed that calves were selected disproportionately to their presence in the population (23.7% versus 11.0%), while bison between two and five years were relatively immune to wolf predation. Bison five years and older were killed at a rate slightly higher than their presence in the population, but this difference was not significant. While such a comparison is not acceptable in absolute terms, it does show trends. In the absence of capturing and marking of bison this comparison has to suffice as a rough estimate.

From 1978 to 1981, winter kills made by the Hornaday River pack consisted of 12 adult male bison, 16 adult females, 3 yearlings, and 17 calves. Comparison of ages of these wolf-killed bison to the estimated age structure of the population (Table 51) revealed a similar pattern of prey

Table 51. Estimated age structure of the bison population in early winter, and bison killed by wolves in winter in Wood Buffalo National Park; 1971 to 1981.

	Number of bison											
	Sweetgrass				Hay Camp				Combined			
Age class (years)	Total[1]	Adjusted total[2]	Percent	Percent killed by wolves (NIW)	Total[3]	Adjusted total[2]	Percent	Percent killed by wolves (HR pack)	Total	Adjusted total	Percent	Percent killed by wolves (total)
Calves	134	218	11.3	18.6	43	23	8.8	35.4	177	241	11.0	23.7
Yearlings	208	198	10.3	0.0	32	35	13.4	6.3	240	233	10.6	7.6
2-4	616	586	30.4	16.3	75	82	31.3	2.1	691	668	30.5	10.7
5-10	966	719	37.3	51.2	112	94	35.8	35.4	1078	813	37.1	42.7
11+	5	208	10.8	14.0	0	28	10.8	20.8	5	236	10.8	15.3
Total	1929	1929	100.1	100.1	262	262	100.1	100.0	2191	2191	100.0	100.0

[1]Novakowski and Choquette (1964).
[2]Based on 1978-1980 mean calf proportion (Hay Camp 8.8%, Sweetgrass 11.3%) from early winter aerial surveys, and adjusted proportion of aged bison (10.8%) in 1971 field slaughter (Currier 1971).
[3]Novakowski and Choquette (1963).
NIW = non-instrumented wolves; kills by these occurred primarily in the Peace-Athabasca delta.

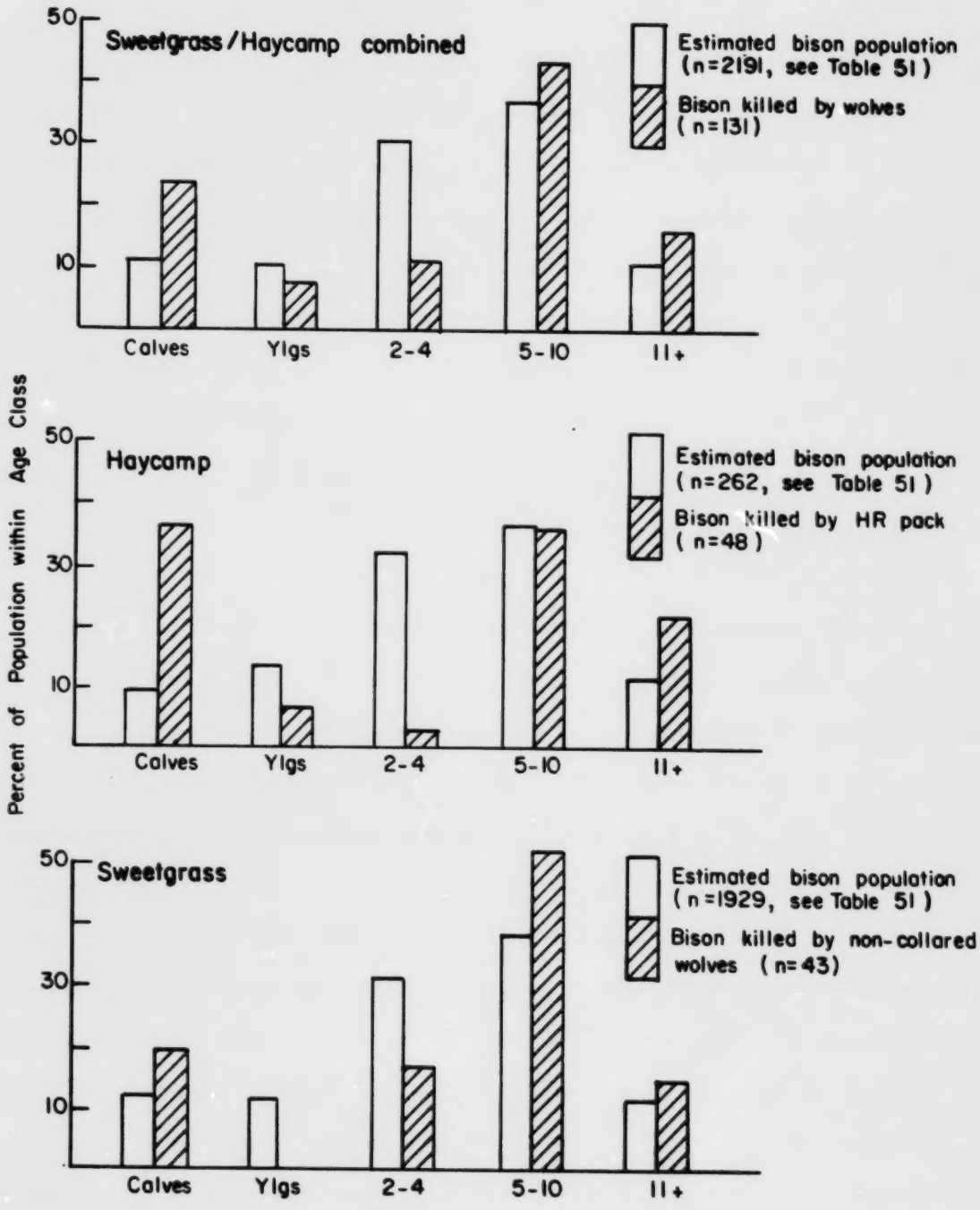


Figure 48. Age distribution of bison population and bison killed by wolves in Wood Buffalo National Park; 1971 to 1981.

selection to that of 1971 to 1981. Predation on calves and old bison (11+ years) was particularly heavy (Fig. 48). The latter pattern was not evident for non-instrumented wolves. Prey selection here for calves was slightly higher than expected (18.6% versus 11.3%), and probably reflected a bias in the sample size, since in a random search, calves are more difficult to spot than adult bison.

Adult male and female bison were killed in proportions to their estimated abundance in the population (104 bulls:108 cows, Novakowski 1958b; 95 bulls:115 cows, Fuller 1951b; 2624 bulls:2687 cows in this study, Table 29), for the 1971-81 kill sample (39:41), Hornaday River pack sample from 1978-81 (12:16), and sample for non-instrumented wolves from 1978-81 (15:19).

Prey selection by the Hornaday River pack for calves versus adult bison (other age and sex classes not determined) was determined from comparisons of available prey based on early winter aerial surveys, and number of calves and adults killed during each winter from 1978-79 to 1980-81 (Table 52). Calves were killed disproportionately by all wolves in the park in all years, except by the Hornaday River pack in 1978-79, which concentrated predation on adults that winter. Prey selection by the Hornaday River pack varied from entirely adult bison in 1978-79 to 50 and 43% calves in 1979-80 and 1980-81 respectively (Table 52). This change was attributed to changing prey availability, winter severity and related bison condition, and the social status of the pack during these years. Conversely, with the exception of 1978-79 by the Hornaday River pack, adult bison in all years were killed less than expected from their observed presence, although the differences between availability and numbers killed

Table 52. Estimated age structure (adults[1]/calves) of the bison population in early winter[2], and bison killed by wolves in winter in Wood Buffalo National Park; 1978-79, 1979-80, and 1980-81.

	Number of bison							
	Hornaday River pack[3]				Non-instrumented wolves[4]			
	Number available	Percent	Number killed	Percent	Number available	Percent	Number killed	Percent
1978-79								
Calves	5	2.9	0	0.0	166	11.5	3	27.3
Adults	174	97.1	12	100.0	1272	88.5	8	72.7
Total	179	100.0	12	100.0	1438	100.0	11	100.0
1979-80								
Calves	69	7.8	11	50.0	200	9.2	2	20.0
Adults	814	92.2	11	50.0	1966	90.8	8	80.0
Total	883	100.0	22	100.0	2166	100.0	10	100.0
1980-81								
Calves	96	11.0	6	42.9	425	12.5	3	14.3
Adults	774	89.0	8	57.1	2969	87.5	18	85.7
Total	870	100.0	14	100.0	3394	100.0	21	100.0
All years								
Calves	170	8.8	17	35.4	791	11.3	8	19.0
Adults	1762	91.2	31	64.6	6207	88.7	34	81.0
Total	1932	100.0	48	100.0	6998	100.0	42	100.0

[1]All bison older than yearlings.
[2]All are early winter counts, except 1978-79 which is midwinter (radio-tracking commenced 9 February 1979).
[3]Hornaday River pack home range: 1978-79 - Hay Camp and Darough Creek prairies.
1979-80 - Raup Lake, Murdock Creek meadows; Hay Camp and Darough Creek prairies.
1980-81 - Raup Lake meadows; Hay Camp and Darough Creek prairies.
[4]All other primary bison ranges.

were less for non-instrumented wolves than for the Hornaday River pack in the winters 1979-80, 1980-81, as well as the 1978-81 aggregate.

The mean composition of marrow fat in femurs collected from 72 wolf-killed bison in the park from winters 1977-78 to 1980-81 (Appendix 8) was 73% and ranged from 7% to 99% (Fig. 49). Mean marrow-fat values for adult males killed were the lowest (67%, n = 25), followed by adult females (76%, n = 32), and calves (81%, n = 12). Marrow-fat values for adult males were significantly less ($p < 0.05$) than those for other age/sex groups (Kingsley 1982). Older age classes of both male and female bison also had lower marrow fat than younger bison (see Fig. 49), and values for old males were lower than those for old females. Marrow-fat values for all bison combined were lowest in 1978-79 (Fig. 50), although those for adult males were lowest in 1979-80. Mean marrow-fat values for bison calves were highest in 1979-80, and did not support our earlier conclusions that calf condition and viability were reduced in years following a severe winter.

Marrow-fat values for wolf-killed bison decreased from early to late winter (Fig. 51), but these changes were not statistically significant (Kingsley 1982). A decrease was most noticeable for adult males, and appeared to reflect an expected decline in condition for the bison population at large as winter progressed, although no data from a random sample of bison were available to verify this hypothesis. Wolf predation on calves was relatively constant throughout the winter (Table 53).

When the condition of wolf-killed male bison, and the apparent ease with which they were killed are considered together, it is conceivable that the nutritional plane of all male bison in the population during winter was considerably lower than that of females and young bison. Adult moose and

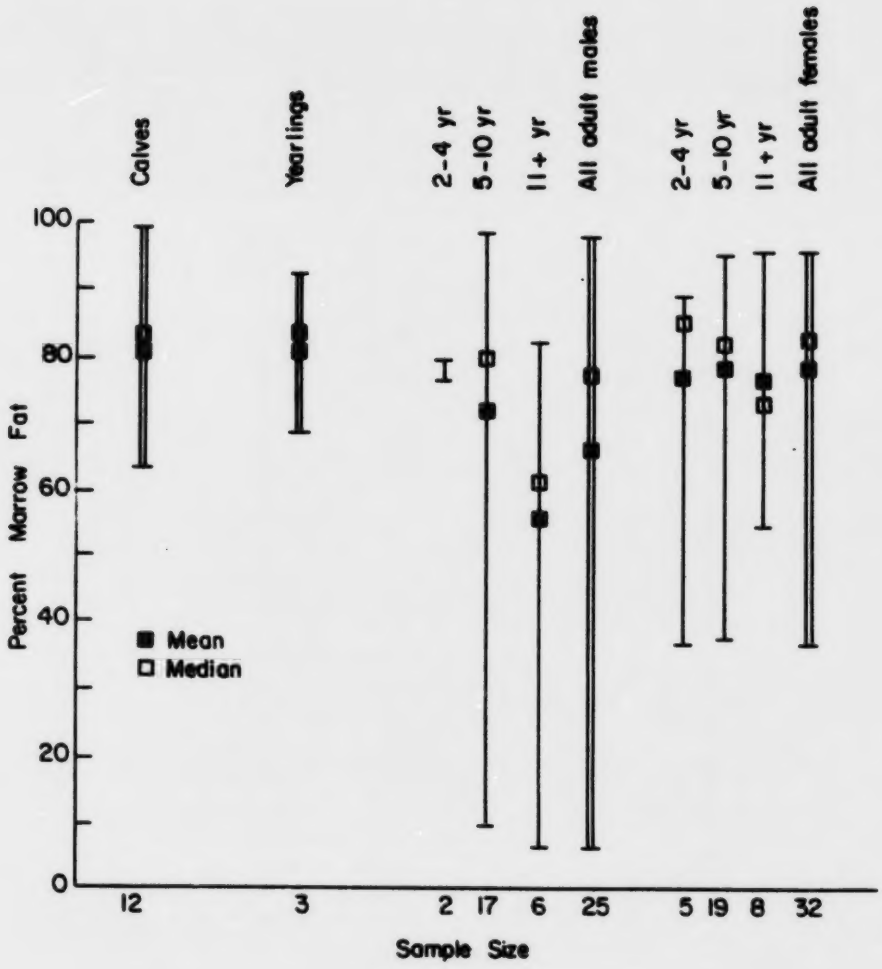


Figure 49. Percent marrow-fat distribution of 72 wolf-killed bison in Wood Buffalo National Park for winters 1977-78 to 1980-81 combined.

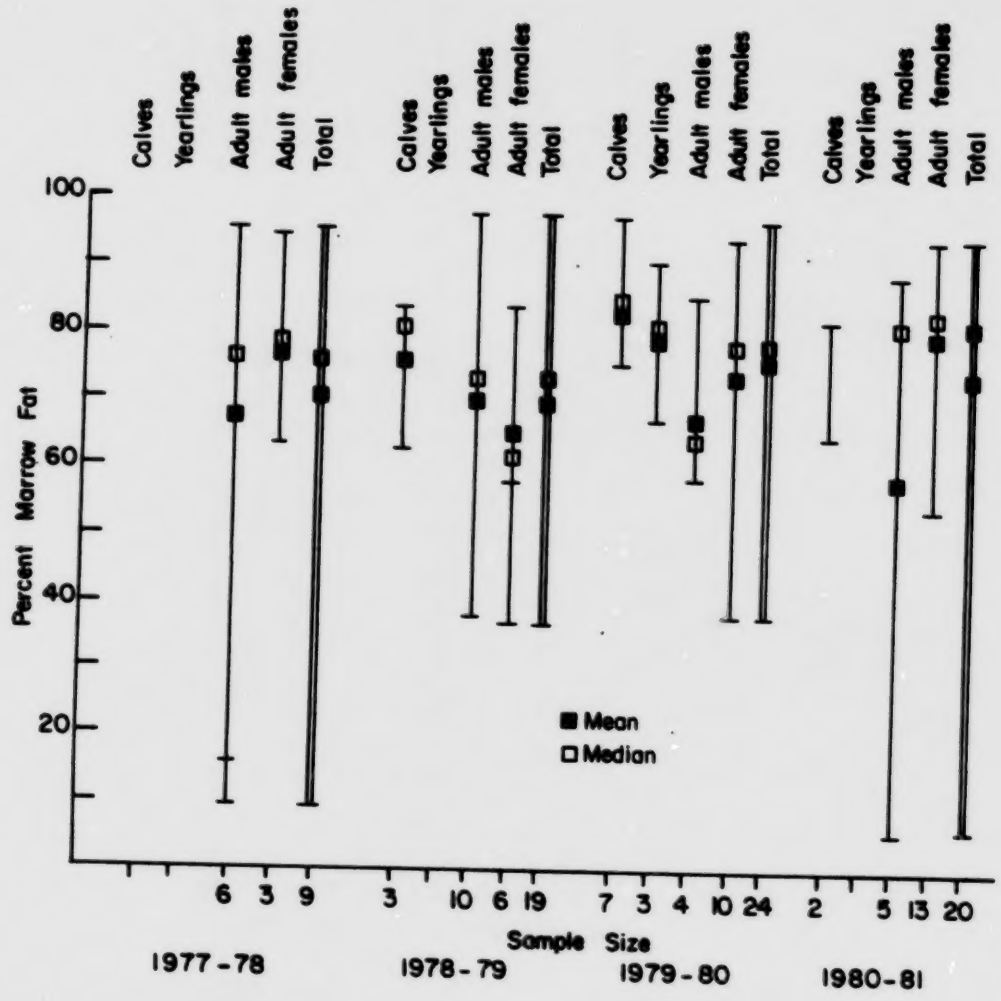


Figure 50. Percent marrow-fat distribution of 72 wolf-killed bison in Wood Buffalo National Park for each winter 1977-78, 1978-79, and 1980-81.

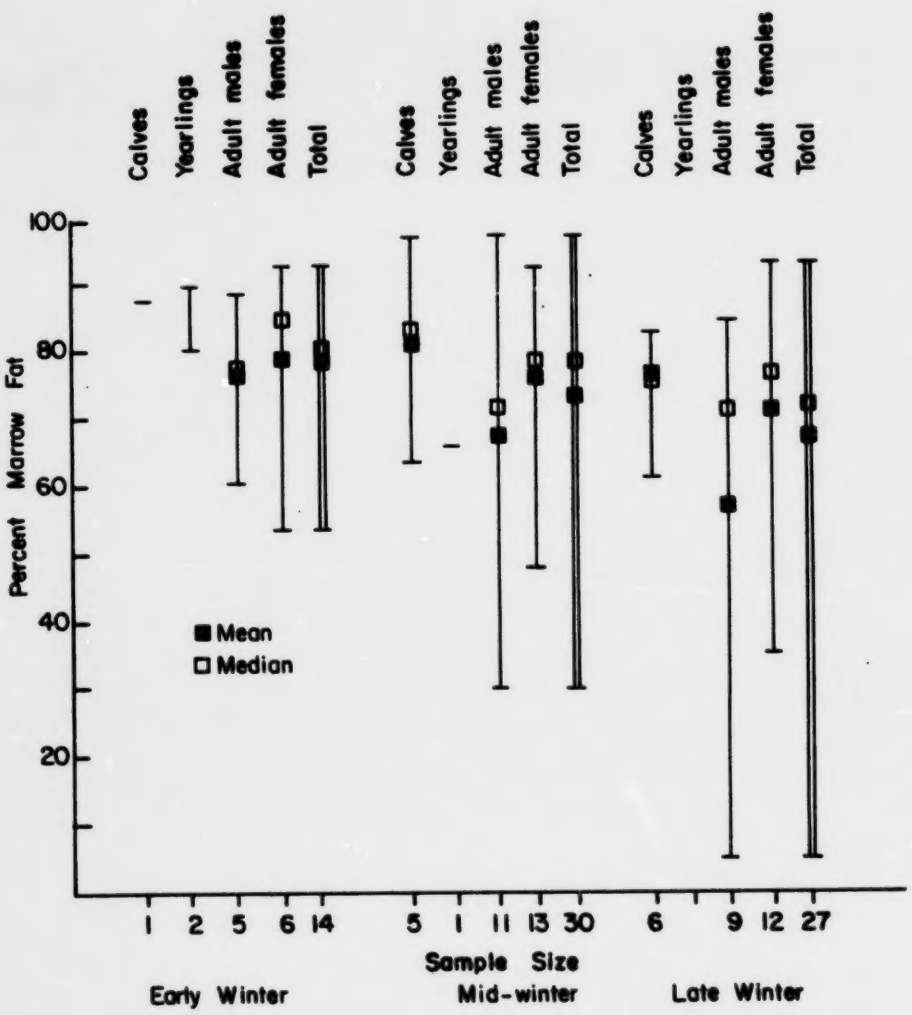


Figure 51. Percent marrow-fat distribution of 72 wolf-killed bison in Wood Buffalo National Park for early, mid, and late winter periods, 1977-78 to 1980-81.

Table 53. Predation rates and prey consumption by the HR pack in Wood Buffalo National Park; 1978-79 to 1980-81.

Year	Intensive monitoring period	No. days	Prey killed and consumed[2]					No. prey killed/day	Mean pack size	Prey biomass/ pack/day[4] (kg)	Prey biomass/ wolf/day[4] (kg)
			Adults		Calves	Ylgs	Total				
			Males	Females							
1978-79	12/02/79-28/02/79 (MW)	17	2	-	-	-	2	0.12	10	64.0	6.4
	01/03/79-31/03/79 (LW)	31	2	2	-	-	4	0.13	10	61.0	6.1
	Total	48	4	2	-	-	6	0.13	10	62.0	6.2
1979-80	14/11/79-27/12/79 (EW)	44	-	1	4	2	7	0.16	12	30.5	2.5
	18/01/80-29/02/80 (MW)	43	2[3]	3[3]	3	1	9	0.21	13	61.2	4.7
	01/03/80-07/04/80 (LW)	38	-	2	4	-	6	0.16	10	35.4	3.5
	Total	125	2	6	11	3	22	0.18	12	40.3	3.4
1980-81	09/12/80-31/12/80 (EW)	23	-	2	-	-	2	0.09	7	35.0	5.0
	15/01/81-28/02/81 (MW)	44	1	2	2	-	5	0.11	8	36.8	4.6
	01/03/81-14/04/81 (LW)	45	1	2	4	-	7	0.15	8	41.6	5.2
	Total	112	2	6	6	-	14	0.12	8	38.4	4.8
Combined winter	Early winter	67	-	3	4	2	9	0.13	10	32.0	3.2
	Midwinter	104	5[3]	5[3]	5	1	16	0.15	10	51.3	5.1
	Late winter	114	3	6	8	-	17	0.15	9	44.9	5.0
	Total	285	8	14	17	3	42	0.15	10	44.2	4.3

[1]Bison older than two years.
[2]Assumes 100% consumption by the HR pack only.
[3]Total includes one adult male moose and one adult female moose.
[4]Based on 80% edibility (Pimlott 1967) of 625 kg for adult male bison, 470 kg for adult female bison, 190 kg for bison calves, 300 kg for bison yearling (H. Reynolds, pers. comm.); 500 kg for adult male moose, and 350 kg for adult female moose (Cowan and Guiget 1976).
EW = early winter; MW = midwinter; LW = late winter.

elk lose much fat reserve during the rut (Yazan 1959; Flook 1970; McGillis 1972); they are unable to recover this substantial loss before the onset of winter, and thus may show the effects of a negative energy balance before females do. Mature male caribou apparently also enter the winter in poorer condition than females (Dauphine 1976). Adult male bison eat sparingly, yet are extremely active during the rut (Lott 1978) and likely enter the winter with lower fat reserves than do other members of the population.

b. Predation rates and prey utilization

During eight periods of intensive aerial tracking of the Hornaday River pack in winters 1978-79, 1979-80, and 1980-81 (total 285 days), the pack killed 40 bison and 2 moose, or an average of one animal every 6.8 days (Table 53). Data on prey utilization in 1978-79 indicated a high degree of consumption of carcasses by the Hornaday River pack (Oosenbrug and Carbyn 1982), and this was also true in the following winters (Table 53). The wolves normally consumed or carried off a bison calf entirely within one day, and did not revisit remains of calf carcasses. Adult bison were not usually totally consumed before being first abandoned by the pack, but in all cases were completely utilized within a month of being killed (Table 54).

The Hornaday River pack spent an average of 2.4 days at each adult bison carcass after first killing it (Table 54). These data are similar to those of Fuller and Keith (1980) where packs of 9-11 wolves remained at kills of adult moose an average 2.5 days and at calf kills an average of 1.5 days. Carcass utilization in that study was also complete. Although other wolves (singles and pairs), as well as smaller scavengers such as foxes and ravens were known to feed on bison carcasses, wolves in the

Table 54. Mean prey utilization rates for the HR pack in Wood Buffalo National Park; winters 1978-79 to 1980-81.

Date of kill	Sex	Age[1]	Estimated amount consumed			No. days pack at kill	No. subsequent relocations at kill[5]
			First examination[3]	Second examination[3]	Third examination[3]		
19/01/79	M	6	2 (1)	4 (43)		1[4]	-[7]
12/02/79	M	9	3 (9)	4 (35)		3	2 (3)
24/12/79	M	7	2 (3)	3 (7)	4 (12)	2	1 (1)
12/03/79	F	7	2 (4)	4 (23)		4	1 (3)
20/03/79	M	10	4 (21)			1	1 (2)
28/03/79	F	11	4 (8)			2	-
31/03/79	M	10	3 (5)	4 (37)		3	-
11/04/79	F	12	4 (2)			2	-
21/04/79	F	-	1 (1)			-[4]	-
14/11/79	F	YLG	4 (2)			-	0
23/11/79	-	YOY	4 (12)			1	0
29/11/79	F	9	4 (7)			2	0
15/12/79	F	YLG	4 (5)			1	0
17/12/79	-	YOY	4 (3)			1	0
22/12/79	-	YOG	4 (26)			1	0
27/12/79	-	YOY	4 (3)			2	0
19/01/80	M	17	4 (26)			2	0
24/01/80	F	9	4 (7)			3	1 (1)
30/01/80	F[6]	4	3 (3)			1	0
31/01/80	F	12	4 (3)			2	0
04/02/80	M[6]	6	4 (3)			2	1 (1)
13/02/80	M	YLG	4 (3)			1	0
17/02/80	-	YOY	4 (10)			1	0
20/02/80	-	YOY	4 (4)			1	0
23/02/80	-	YOY	4 (2)			1	0
02/03/80	M	YOY	3 (2)	4 (8)		2	0
10/03/80	-	YOY	4 (4)			1	0
13/03/80	-	YOY	4 (1)			1	0
23/03/80	F	9	4 (7)			3	0
27/03/80	F	8	4 (3)			2	0
06/04/80	-	YOY	-			-	0

Table 54. (Continued).

Date of kill	Sex	Age[1]	Estimated amount consumed			No. days pack at kill	No. subsequent relocations at kill[5]
			First examination[3]	Second examination[3]	Third examination[3]		
09/12/80	F	14	4 (6)			2	0
28/12/80	F	17	4 (2)			3	1 (1)
15/01/81	-	YOY	4 (9)			1	0
20/01/81	F	8	4 (4)			2	0
04/02/81	M	15	4 (11)			3	1 (1)
15/02/81	F	8	2 (1)	4 (20)		4	0
25/02/81	-	YOY	4 (6)			1	0
02/03/81	-[7]	YOY	4 (1)				
08/03/81	-	YOY	4 (1)			1	0
13/03/81	F	3	4 (4)			1	0
19/03/81	-	YOY	4 (1)			2	0
24/03/81	F	12	2 (1)	4 (11)		1	0
28/03/81	M	16	3 (3)	4 (16)		2[4]	1 (1)
13/04/81	-	YOY	4 (1)			2	0
						1	0

[1]Age of adult bison determined by sectioning of incisors.
[2]Percent of edible portions consumed.
1 = 0-25%
2 = 26-50%
3 = 51-75%
4 = 76-100%
[3]Figures in brackets are number of days between date of examination and date of kill.
[4]Wolves prematurely left kill due to human disturbance.
[5]Radiolocations do no accurately reflect follow-up utilization of bison kills; figures in brackets are number of days pack was known to revisit former kills.
[6]Adult moose.
[7]No data available.

Hornaday River pack were considered the major consumers of the bison they killed.

Biomass calculations were based on live weights of bison (H. Reynolds, pers. comm.), and it was assumed that 80% of any carcass was edible (Pimlott 1967). Mean pack size was used to determine the prey biomass consumed per wolf per day, and this varied from 2.5 kg in early winter 1979-80 to 6.4 kg in midwinter 1978-79 (Table 53). The Hornaday River pack scavenged on four bison carcasses in 1978-79, two in 1979-80, and none in 1980-81. The cause of death of five of these was unknown; the other was killed by an adjacent pack (Salt River) which was displaced from the kill by the Hornaday River pack in late February 1980. In all cases 75 to 100% of each carcass was already consumed when the pack visited them, and thus were considered to contribute little to the overall amount of food required by the pack during these periods of observation.

Prey biomass consumption was considerably higher in 1978-79 than in 1979-80 or 1980-81 (6.2 versus 3.4 and 4.8 kg per wolf per day). The difference could be attributed to the severe winter of 1978-79. Although the rate at which bison were killed was higher in 1979-80 than in the other winters, selection was primarily for calves, which reduced the per capita biomass consumed. Unlike wolf-killed deer in Minnesota (Mech 1977a) and elk in Manitoba (Carbyn 1980), there was no significant increase in predation rate or biomass consumption from early to late winter in any year.

Predation rates by the Hornaday River pack were similar to those by wolves in the Slave River lowlands. Van Camp (1980) reported that over a six-week period in early winter, a pack of 12-14 wolves consumed a minimum

of six bison, or approximately one per week, although he felt that the winter predation rate for each pack (average size 11 wolves) more closely approached one adult every nine days, as well as one calf every 15 days.

The data from this study indicated that over three winters each wolf in the Hornaday River pack consumed an average 4.3 kg per day, and were similar to those of Peterson (1977) who calculated winter food availability to vary from 6.2 to 10.0 kg per wolf per day during 1971-73, and 4.4 to 5.0 kg during 1974 on Isle Royale. Peterson suggested that when degree of utilization was unknown, a measure of food availability rather than food consumption was obtained. Since our data described virtually complete utilization of kills by the Hornaday River pack (Table 54), food availability in our case approached or equalled consumption.

Our results on food consumption were somewhat higher than those published for wolves preying on deer. In Ontario Pimlott et al. (1967) and Kolenosky (1972) estimated a daily rate of consumption of 3.81 and 2.93 kg per wolf, and Mech and Frenzel (1971) calculated a rate of consumption in northeastern Minnesota of 2.74 kg per wolf per day. However, on Isle Royale wolves preying on moose were found to consume an average of 5.6 kg per wolf per day over three winters of observation (Mech 1966). In Riding Mountain National Park wolves and scavengers (to an unknown degree) consumed 6.7 kg of prey per wolf per day under unusual severe winter conditions and high elk densities (Carbyn 1981).

Differences in food consumption between the various study areas mentioned may be partially explained by size differences and energy requirements of the wolves under study. Based on the weights of our captured animals (Appendix 1), wolves in the Hornaday River pack weighed an average

of 43 kg and were substantially larger than those found in eastern North America. However, differences in food consumption may be more due to annual variation in prey vulnerability and abundance (Peterson 1977).

Data from this study supporting a direct relationship between pack size and prey consumption are inconclusive. Predation rates were highest in 1979-80 when the Hornaday River pack was largest, but the actual prey biomass consumed by each pack member was lowest that winter, suggesting that abundance and vulnerability of bison were the dominant factors which determined bison consumption by wolves, rather than pack size. Prey biomass consumption by the Hornaday River pack was similar in 1979-80 and 1980-81 winters when pack size differed the most.

c. Food habits determined from scat analysis

Analysis of wolf scat data was based on percentage frequency occurrence of recovered food items in the scat samples, and on calculations of relative biomass and numbers of different prey species using a linear regression developed by Floyd et al. (1978). Volume of food items in each scat or relative estimated bulk (Fritts and Mech 1981) was not determined, however, multiple food items in one scat were uncommon (9.1% of total sample) and were not consistently associated with the same food items. Differences in frequency occurrence between weighted frequencies (Carbyn 1980) and unweighted frequencies were not significant ($p > 0.05$). Thus total food items were considered an adequate representation of prey types as discrete components of scat samples, and were used synonymously in the biomass calculations.

Bison was generally the most important food of wolves in Wood Buffalo National Park in winter and summer, both in terms of frequency

occurrence of food items (Table 55) and biomass consumed (Table 56). Of 1025 winter and 2166 summer food items recovered from 2928 scat samples (Appendix 9), bison comprised 55% and 13% respectively. The occurrence of bison in winter scats was significantly higher ($p < 0.05$) than in summer, and the estimated relative bison biomass consumed was approximately 4 times greater in winter. When estimated weights of bison and moose were arbitrarily adjusted downward by 50% to reflect predation of young of the year, bison biomass consumed was approximately 8 times greater in winter than in summer. Lesser differences were noted in percent of relative biomass consumed, as bison comprised about 82% of mammal biomass in winter compared to about 67% (57% adjusted) in summer.

Wolf scat information for other areas containing bison exists only for the Slave River lowlands, adjacent to the park. There bison occurred in 51% of scat samples in winter and 14% in summer (Van Camp 1980). Biomass consumption of bison was also similar to our results, in that the species comprised 80% of total relative biomass consumed in winter, and 69% in summer. Elsewhere studies of wolf scat contents have indicated that moose in Alaska (Ballard et al. 1981) and Alberta (Fuller and Keith 1980), deer in the Great Lakes region (Pimlott et al. 1969; Van Ballenberghe et al. 1975; Fritts and Mech 1981), and elk in Manitoba (Carbyn 1980) are the major food sources for wolves in winter.

There was a significant decrease ($p < 0.05$) in occurrence of bison in scats between the summers 1977 and 1978, and 1979 and 1980. The decrease may be partially explained by a greater sampling of wolf dens and rendezvous sites during the latter two summers (Table 57) where bison occurrence in scats was particularly infrequent, and occurence of small mammals such as muskrat (Ondatra zibethica) and snowshoe hare (Lepus americanus) was

Table 55a. Percentage occurrence of food items in scats collected in summer (May to October) of each year from 1977 to 1980 in Wood Buffalo National Park.

Species	1977	1978	1979	1980	Total
Bison	29.3	19.6	7.2	10.8	13.3
Moose	0.9	2.4	2.8	2.1	2.3
Muskrat	15.4	15.5	34.6	42.4	29.8
Beaver	6.3	6.7	14.0	11.6	10.8
Snowshoe hare	13.6	37.1	28.6	20.5	26.5
Microtine	7.7	2.4	1.2	0.8	2.0
Porcupine		2.8	1.4	0.5	1.3
Squirrel	4.1		1.8	0.6	1.3
Waterfowl/grouse	11.8	9.5	5.4	6.8	7.3
Vegetation	9.5	2.4	1.3	0.2	2.0
Unidentified	1.4	1.6	4.7	3.6	3.3
Total food items	221	496	791	658	2166
Total scats	158	433	738	616	1945

Table 55b. Percentage occurrence of food items in scats collected in winter (November to April) of each year from 1976-77 to 1979-80 in Wood Buffalo National Park.

Species	1976-77	1978-78	1978-79	1979-80	Total
Bison	53.8	48.1	53.2	60.8	54.9
Moose	3.1	8.6	9.3	10.4	9.2
Muskrat	23.1	12.3	6.2	2.2	6.6
Beaver	1.5	2.5	2.2	1.8	2.0
Snowshoe hare	4.6	19.8	21.8	12.9	18.1
Microtine	4.6		0.3	1.4	0.9
Porcupine			1.7	1.8	1.5
Squirrel			0.3		0.2
Waterfowl/grouse	1.5		0.3	1.4	0.7
Vegetation	7.7	8.6	2.7	0.4	2.8
Unidentified			2.0	6.8	3.0
Total food items	65	81	601	278	1025
Total scats	56	71	582	274	983

Table 56. Estimated relative biomass and numbers of mammalian prey consumed, as determined from frequeny occurrence of food items in scats collected in winter and summer from 1977 to 1980 in Wood Buffalo National Park.

Species	Estimated weight of prey (kg)	Relative frequency of prey in scats	Relative biomass consumed[4]	Percent biomass consumed	Relative number of prey consumed	Ratios of prey consumed
Winter		n = 1025				
Bison	383.00[1]	54.9	441.40	82.4	1.15	1.00
Moose	425.00[2]	9.2	81.70	15.3	0.19	0.17
Muskrat	1.50[3]	6.6	2.71	0.5	1.81	1.57
Beaver	12.50[3]	2.0	1.26	0.2	0.11	0.10
Snowshoe hare	1.20[3]	18.1	7.31	1.4	6.10	5.30
Microtine	0.04[3]	0.9	0.34	0.1	8.56	7.44
Porcupine	10.00[3]	1.5	0.87	0.2	0.09	0.08
Squirrel	0.80[3]	0.2	0.08	0.0	0.10	0.09
Summer		n = 2166				
Bison	383.00	13.3	106.93	67.2	0.28	1.00
Moose	425.00	2.3	20.42	12.8	0.05	0.18
Muskrat	1.50	29.8	12.22	7.7	8.15	29.11
Beaver	12.50	10.8	6.80	4.3	0.54	1.93
Snowshoe hare	1.20	26.5	10.71	6.7	8.92	31.86
Microtine	0.04	2.0	0.76	0.5	19.04	68.00
Porcupine	10.00	1.3	0.75	0.5	0.08	0.29
Squirrel	0.80	1.3	0.51	0.3	0.64	2.29
Summer		n = 2166				
Bison	191.50[5]	13.3	55.60	56.9	0.29	1.00
Moose	212.50[5]	2.3	10.65	10.8	0.05	0.17
Muskrat	1.50	29.8	12.22	12.4	8.15	28.10
Beaver	12.50	10.8	6.80	6.9	0.54	1.86
Snowshoe hare	1.20	26.5	10.71	10.98	8.92	30.76
Microtine	0.04	2.0	0.76	0.8	19.04	65.70
Porcupine	10.00	1.3	0.75	0.8	0.08	0.28
Squirrel	0.80	1.3	0.51	0.5	0.64	2.21

[1]Based on known age ratio in winter kill of 8 adult males, 14 adult females, 17 calves and 3 yearlings with respective weights of 625, 470, 190 and 300 kg (H. Reynolds, pers. comm.).
[2]Based on known sex ratio in winter kill of 1 adult male: 1 adult female with respective weights of 500 and 350 kg (Cowan and Guiget 1976).
[3]Carbyn and Kingsley (1980).
[4]Floyd et al. (1978). Biomass consumed calculated from regression equation $Y = 0.38 + 0.02X$.
[5]Adjusted weights for bison and moose to reflect predation on young of the year.

Table 57. Percent frequency occurrence of food items in scats collected at dens and rendezvous sites from 1978 to 1980 in Wood Buffalo National Park.

Dens / Species	Hornaday River 1978	Salt River 1979	Lake Claire 1978	Lake One 1978	Lake One 1979	Lake One 1980	Mean
Bison	10.1	1.9	19.6	9.8	0.5		1.5
Moose	6.0	7.6					
Muskrat	13.1	40.0	41.2	17.1	34.6	60.2	40.4
Beaver	5.4	29.5	13.7	14.6	4.9	15.5	9.4
Snowshoe hare	43.5	19.0	11.8	34.1	41.6	15.5	32.5
Microtine	0.6	1.9		7.3	1.1		1.5
Porcupine	2.4			7.3	1.1		1.5
Squirrel					3.2		1.8
Waterfowl/grouse	11.3		9.8	9.8	3.8	8.7	6.1
Vegetation	6.5		2.0		3.2		1.8
Unidentified	1.2		2.0		6.0		3.3
Total food items	168	105	51	41	185	103	329
Total scats	138	105	49	35	171	99	305

Table 57. (Continued).

Rendezvous sites / Species	Halfway meadow[1] 1979	Lake One 1978	1979	1980	Mean
Bison	2.1	20.7	22.6	3.6	9.4
Moose			2.2		0.4
Muskrat	57.4	8.6	19.4	48.3	37.9
Beaver	2.1	3.4	16.1	10.3	10.6
Snowshoe hare	6.4	34.5	23.7	19.5	22.1
Microtine		5.2	2.2	0.9	1.7
Porcupine	4.3	1.7		0.6	0.6
Squirrel			4.3	1.2	1.7
Waterfowl/grouse	19.1	13.8	2.2	9.1	7.9
Vegetation		10.3	3.2	0.3	2.5
Unidentified	6.4	1.7	4.3	5.6	5.2
Total food items	47	58	93	329	480
Total scats	38	44	86	297	427

[1]Occupied by the Lake Claire pack in 1979.

high. It is also possible that muskrat and hare populations increased substantially between those years, (Jalkotzy and Oosenbrug 1982) and were included in the wolves' diet in relation to their abundance. In comparison to previous summers, bison were conspicuously absent from Lake One during 1980 (Carbyn et al. 1981), the area from which the major portion of scat samples was derived. The occurrence of bison in summer scats increased from about 10% in May-June to 12% in July-August to 32% in September-October, and probably reflected increased pack mobility and greater availability of bison calves as the summer progressed.

In terms of frequency occurrence of eight mammal species, moose ranked third in winter and fifth in summer (see Table 55). Biomass calculations indicated that after bison, moose contributed the greatest biomass consumed in both winter and summer. This was largely due to the estimated weight of moose which was based on the known kill ratio in winter (Table 56). With adjusted weights in summer, muskrat and snowshoe hare became more important.

Among the small mammal species snowshoe hare ranked first overall throughout the year. In terms of both frequency occurrence and biomass consumed, muskrat was the major prey item in summer. Due to differences in estimated weight, hare was consumed in greater numbers than muskrat. For every one bison consumed, it appeared that approximately 5, and 32 hare were consumed in winter and summer respectively. Respective figures for muskrat were 1.5 in winter and 29 in summer.

Beaver (Castor canadensis) occurrence in scats was low compared to other areas (Pimlott et al. 1969; Voigt et al. 1976; Peterson 1977), but as beaver hair is sometimes difficult to differentiate from muskrat hair

(Fuller and Keith 1980; Kennedy and Carbyn 1981), the importance of beaver remains unclear. Beaver was more common in summer than in winter scats (Tables 55a, 55b), and the data indicate that this species was less frequent in late summer than in early and midsummer scats, and became more frequent in late winter. It is possible that beaver are less vulnerable to wolf predation as the summer progresses. Although the occurrence of beaver in winter scats was low (2.0% compared to 11% in summer), the greatest winter occurrence was in March-April (Table 56) when beavers are more active and may be vulnerable outside their dens. This situation was also documented in Algonquin Park (Pimlott et al. 1969; Theberge et al. 1978), and apparently sometimes occurs even in midwinter (Peterson 1977; Carbyn 1980).

Other small mammals comprised a minor portion of occurrences in wolf scats and biomass of total prey consumed, although microtines by virtue of their small size contributed the largest relative number of prey consumed (Table 59). Birds (waterfowl/grouse) were not included in biomass estimates because the regression equation is applicable to mammals only. The frequency occurrence of birds in scats (Tables 58a, 58b) suggested that they may have been seasonally important food items in the vicinity of dens and rendezvous sites.

Analysis of scats (adults and pups combined) collected at four denning localities and two rendezvous sites from 1978 to 1980 revealed considerable variation between areas and from year to year (Table 57). As in the entire summer sample, muskrat occurrence in scats collected at Lake One dens and rendezvous sites increased from 1978 to 1980. With the exception of the Hornaday River den in 1978, muskrat was also an important

Table 58a. Percentage occurrence of food items in scats collected in early, mid, and late summer over the years 1977 to 1980 in Wood Buffalo National Park.

Species	Early summer (May-June)	Midsummer (July-August)	Late summer (September-October)
Bison	9.6	11.7	31.6
Moose	3.2	1.1	3.3
Muskrat	30.5	33.5	13.5
Beaver	11.3	12.6	3.3
Snowshoe hare	32.8	19.3	30.9
Microtine	0.8	2.7	3.6
Porcupine	1.5	1.3	0.7
Squirrel	0.9	2.0	0.4
Waterfowl/grouse	5.6	9.2	6.5
Vegetation	0.9	2.0	4.4
Unidentified	3.0	4.0	1.8
Total food items	930	966	275
Total scats	873	842	230

Table 58b. Percentage occurrence of food items in scats collected in early, mid, and late winter over the years 1977 to 1980 in Wood Buffalo National Park.

Species	Early winter (November-December)	Midwinter (January-February)	Late winter (March-April)
Bison	62.8	62.2	48.6
Moose	7.4	14.1	6.7
Muskrat	4.1	2.2	9.9
Beaver	0.7	0.6	3.2
Snowshoe hare	14.2	12.5	22.7
Microtine	0.7	0.3	1.3
Porcupine		1.9	1.6
Squirrel		0.3	0.2
Waterfowl/grouse			1.3
Vegetation	6.8	1.6	2.5
Unidentified	3.4	4.4	2.2
Total food items	148	320	556
Total scats	140	311	528

Table 59. Percentage frequency occurrence of food items in scats collected at and away from dens and rendezvous sites in Wood Buffalo National Park during 1978 to 1980.

Species	At dens and rendezvous sites	Away from dens and rendezvous sites	
		May-August	May-October
Bison	6.8	17.2	21.2
Moose	1.7	3.0	3.0
Muskrat	36.2	25.3	22.0
Beaver	11.0	13.4	10.5
Snowshoe hare	26.6	24.6	26.4
Microtine	1.4	2.4	2.7
Porcupine	1.2	1.7	1.4
Squirrel	1.2	1.8	1.4
Waterfowl/grouse	7.9	6.6	6.6
Vegetation	2.4	0.6	1.6
Unidentified	2.3	3.5	3.0
Total food items	1180	711	986
Total scats	1065	650	880

summer food item at the other dens (Lake Claire 1978, Salt River 1979) and rendezvous site (Halfway meadow 1979). Variations in bison occurrence in scats at dens and rendezvous sites probably resulted primarily from differences in bison abundance in the vicinity of the homesites, but other factors such as the social structure of the packs and artifacts from small sample sizes complicate the situation.

Occurrence of bison in scats collected at dens and rendezvous sites differed significantly ($p < 0.05$) from that in scats collected on trails and roadways away from known homesites (see also Jalkotzy and Oosenbrug 1982). Bison comprised about 7% of food items in scats collected at homesites, and 17% away from homesites from May to August (Table 59). Bison occurred in 21% of food items in scats collected over the entire summer (May to October). Similar conclusions for deer were reported by Theberge et al. (1978) and for elk (Scott and Shackleton 1980). Carbyn (1980) and Fuller and Keith (1980) reported no significant differences in scats collected at dens versus away from dens and rendezvous sites, although in the latter study small mammals (muskrat and beaver) occurred more often in pup scats.

In summary, ungulates (bison and moose together) comprised the bulk of the diet of wolves which were studied in Wood Buffalo National Park both in winter and summer, at least in terms of relative biomass consumed (88% in winter, 80% in summer). Frequency occurrence of muskrat and snowshoe hare was greater than of bison in summer, as were relative numbers of all small mammals except porcupine (Erethizon dorsatum). Shifts for bison were apparent from lower occurrences in early summer to higher occurrences in late summer. These shifts may have been a result of increasing mobility of wolf packs, availability of calves, and changes in bison maternal behaviour

with the onset of the rut. Muskrat and beaver in the diet correspondingly decreased as the summer progressed. The use of small mammals, primarily muskrat, appeared to be tied in to occupation of dens and rendezvous sites, and bison were less important at homesites than in areas away from homesites.

4. Impact of wolf predation on the bison population

Information collected during this study was meant to test the hypothesis stated earlier that "wolf predation was an important influence on bison numbers in the park." Conclusions about wolf numbers, predation rates and prey selection were based primarily on observations of the Hornaday River pack, a group of 8-12 wolves occupying a major portion of primary bison ranges north of the Peace River.

Within the area occupied by the Hornaday River pack during winters 1978-79 to 1980-81, the impact of predation by these wolves was assessed by comparing the proportion of bison killed by the pack over each winter to the recruitment of yearlings into the bison population (Table 60). Prey availability was calculated from the annual midwinter total count survey conducted by members of the park Warden Service and the authors (Appendix 10). Adult bison were defined as those older than one year. The Hornaday River pack killed a mean of 4.0% of the adult bison over the three winters, while recruitment averaged 7.8%.

As bison availability within the home range of the Hornaday River pack was inconsistent and unpredictable throughout the course of the winter a model was computed of the impact of wolf predation over the entire primary bison ranges. This approach was considered to be more accurate

Table 60. Number of available bison, and bison killed by the Hornaday River pack in winters 1978-79 to 1980-81, Wood Buffalo National Park.

	1978-79	1979-80	1980-81	Total
Mean pack size	10	12	8	($\bar{x}$ = 10)
Available prey[1]				
Calves	5	30	57	92
Adults	174	457	656	1287
Bison killed[2]				
Calves	0	16	9	25
Adults	23	16	13	52
Percent killed				
Calves	0.0	53.3	15.8	27.2
Adults	13.2	3.5	2.0	4.0
Recruitment of new yearlings(%)[3]	9.7	5.4	8.3	($\bar{x}$ = 7.8)

[1]Based on midwinter total count within the Hornaday River pack's home range
1978-79 - Hay Camp and Darough Creek meadows
1979-80 - Raup Lake, Hay Camp, Darough Creek, and Murdock Creek meadows
1980-81 - Raup Lake, Hay Camp, and Darough Creek meadows (Appendix 10).
[2]Based on predation rate calculated in Table 53.
[3]Extrapolated proportion of new yearling over entire primary bison ranges, based on mean monthly decreased over first year of life (Table 31).

since it minimized the effect of ingress and emigration of bison from a more restricted area (Hornaday River pack home range), and facilitated the use of survey data for total bison numbers and seasonal changes in calf proportions.

A composite mode of the bison population on the primary bison ranges of Wood Buffalo National Park (Table 61) was based on mean values derived from population trends from February 1978 to April 1981 (Appendix 11). Observed values for calf survival, and arbitrary values for adult mortality were entered at various intervals throughout the year and the resultant population figures were calculated from these entries. Arbitrary values for adult mortality used were those which resulted in the best fit to the observed population estimates obtained by aerial surveys in midwinter of each year as described similarly for models of Alaskan caribou populations (Doerr 1980).

Accordingly, adult mortality in summer (May-October) was set at 2.5% in 1978, 1979, and 1980, and in winter (November-April) was set at 10% in 1978-79 and 5% in 1979-80 and 1980-81. Estimates of total bison numbers in the park based on aerial surveys conducted by the Warden Service were generally considered to be approximately 90% of the actual population (Couchie 1979; Oosenbrug et al. 1981), thus the population figures used in the model are 10% greater than the values obtained from aerial surveys. The total count survey in 1981, however, was in our opinion and that of Warden Anions, considered to be the most accurate on record, and the adult mortality rate for 1980-81 was set to reflect an agreement between our calculated population figure and that of the midwinter aerial survey.

As shown in Table 61, the composite model of the bison population in Wood Buffalo National Park suggested that the population was stationary or

Table 61. Composite one year model[1] of bison population in primary bison ranges of Wood Buffalo National Park, based on bison demography from 30 April 1978 to 30 April 1981.

		Adults[2]	Calves	Population size
Population estimate (30 April)				4575
Calf proportion: May	(16.0%)	4575	750(+750)	5325
Aug.	(13.4%)	4575	714(-36)	5289
Adult mortality:				
May-Oct, (2.5%)		4460(-115)	714	5174
Calf proportion: Nov.	(10.5%)	4460	524(-190)	4984
Adult mortality:				
Nov.-Feb. (3.3%)		4311(-149)	524	4835
Calf proportion: Feb.	(8.9%)	4311	421(-103)	4732
Adult mortality:				
Mar.-Apr. (3.3%)		4167(-144)	421	4588
Calf proportion: Apr.	(7.8%)	4167	353(-68)	4520

[1]As derived from Appendix 11.
[2]Bison older than one year.

declining slightly from 1978 to 1981. If the arbitrary adult mortality rates, and the proportion of calves observed on aerial surveys are accurate, then the large number of adult bison, and the small number of calves that died in winter 1978-79 (Table 62) are consistent with similar wolf predation on these age groups that year. Calf losses appeared to be particularly high in summer 1980, but numbers killed by wolves were similar to 1979-80.

The number of bison killed by wolves (Table 62) was based on the observed predation rates and prey selection by the Hornaday River pack in winters 1978-79, 1979-80, and 1980-81, and the biomass consumed was based on data derived from 1977-80 pooled summer scat data. Bison numbers killed in winter were extrapolated over 180 days (November-April) and assumed a wolf population of 110 over the entire primary bison ranges. Summer kills were calculated from the estimated average daily requirement of wild wolves of 1.7 kg per day per wolf (Mech 1977a) over 185 days (May-October) for 110 wolves.

Given 34 595 kg of edible food needed to sustain 110 wolves (assuming 1.7 kg per day per wolf can be considered an approximation for both adults and pups - see Fuller and Keith 1980), 67.2% consisted of bison (Table 56), and approximately 80% of any bison was edible (Pimlott 1967), then the bison biomass consumed in summer was 27 897 kg (0.672 X 34 595 X 1.2). On the basis of winter prey selection (assumes summer selection was similar), and the respective weights of prey bison (1.47 adult bison older than 1 year: 1 calf, with weights of 465 and 190 kg respectively), 110 wolves killed an average of 32 calves (27 897/(465 X 1.47) + (190 X 1.00),

Table 62. Estimated bison mortality, and number of bison killed by wolves on primary bison ranges of Wood Buffalo National Park, 1978 to 1981.

	Number of bison died[1]			Number of bison killed by wolves[2]		
	1978-79	1979-80	1980-81	1978-79	1979-80	1980-81
Adults						
Summer	117	114	112	47	47	47
Winter	445	219	217	248	145	177
Total	562	323	329	295	192	224
Calves						
Summer	265	84	329	32	32	32
Winter	99	187	225	0	145	133
Total	364	261	564	32	177	165
Total bison						
Summer	382	198	441	79	79	79
Winter	544	406	442	248	290	310
Total	926	604	883	327	369	389

[1]Adult mortality based on arbitrary rates: 1978-79 - summer 2.5%, winter 10%; 1979-80 - summer 2.5%, winter 5%; 1980-81 - summer 2.5%, winter 5%. Calf mortality based on aerial survey results.

[2]Summer predation rates based on biomass consumed as per 1977-1980 pooled scat data, and projected for estimated wolf population of 110 and 1.7 kg/day/wolf requirement (Mech 1977a) over 185 days. Winter kills based on projected predation rates (Table 53) applied to 110 wolves.

and 47 adult bison (32 X 1.47). The number of calves killed by wolves in summer would be considerably higher if calf weights were consistantly less than 190 kg.

A comparison of annual recruitment and proportion of adult bison killed annually by wolves (Table 63) indicated that wolf predation of adult bison in some years (e.g. 1980-81) nearly equalled recruitment of yearlings into the population (assuming that wolf-predation mortality was totally additive). Evidence of the extent to which wolf-predation mortality is compensatory in ungulate populations is virtually nonexistent, although most of the earlier literature implied a high, but unspecified proportion of wolf predation as compensatory (Pimlott 1967; Pimlott et al. 1969; Mech and Frenzel 1971), in that wolves selectively killed the old, very young, and otherwise disabled portion of the population, i.e. animals which most likely would have died anyway. More recent studies (Peterson 1977; Mech and Karns 1977; Fuller and Keith 1980; Hauge and Keith 1981; Gasaway et al. 1983) have indicated that wolf-predation mortality may be at least partially additive, and in combination with severe winters and decreasing forage availability for ungulates, can effectively limit the growth of, or reduce the ungulate population.

In the primary bison ranges of Wood Buffalo National Park, annual bison losses, as derived from the composite model of the population (Table 61), were 408 animals, and recruitment of yearlings was 353, resulting in a net decline of 55 bison (Table 64). The number of bison killed by wolves was calculated for wolf population estimates of 84, 110, and 136 with wolf-predation mortality at either 100% compensatory, 100% additive, or 58% (calves) and 63% (adults) additive. Winter kills were extrapolated from predation rates and prey selection during 1979-80 and 1980-81 only,

Table 63. Annual recruitment of yearlings into the bison population, and proportion of adults[1] killed annually by wolves; primary bison ranges, Wood Buffalo National Park.

	1978	1979	1980	1981
Number of adults in population on 30 April	4685	4565	4474	4522
Number of new yearlings recruited into the population as of 30 April	479(10.2)[2]	443(9.7)	242(5.4)	375(8.3)
Number of adults killed by wolves over one year up to 30 April of next[3]	295(6.3)	192(4.2)	224(5.0)	

[1]Bison older than one year (see Appendix 11 for details).
[2]Percentages in brackets.
[3]Based on 110 wolves and their food requirements, predation rates and assumes wolf predation mortality is 100% additive.

Table 64. Bison mortality, and effects of removal of wolf predation on growth of the bison population, primary bison ranges, Wood Buffalo National Park.

	Total recorded[1]	Number of bison killed by wolves[2]								
		Predation mortality 100% compensatory			Predation mortality 58, 63% additive[3]			Predation mortality 100% additive		
Number of wolves[4]		84	110	136	84	110	136	84	110	136
Calf deaths										
Summer	226	0	0	0	14	19	23	24	32	40
Winter	170	0	0	0	61	81	100	106	139	172
Total	396	0	0	0	75	100	123	130	171	212
Adult deaths										
Summer	114	0	0	0	23	30	37	36	47	58
Winter	294	0	0	0	77	101	125	123	161	199
Total	408	0	0	0	100	131	162	159	208	257
Proportion of adults killed by wolves (%)		0.0	0.0	0.0	2.2	2.9	3.5	3.5	4.5	5.6
Recruitment rate (%)	7.8	7.8	7.8	7.8	9.1	9.5	9.9	10.0	10.7	11.3
Yearlings added	353	353	353	353	428	453	476	483	524	565
Adult losses	408	408	408	408	308	277	246	249	200	151
Net population growth	-55	-55	-55	-55	+120	+176	+230	+234	+324	+414

[1]Calves - composite figures from aerial surveys; adults - composite mortality rates, 1978-81, summer 2.5%, winter 6.6% (see Table 62 for details).
[2]Based on mean of 1979-80 and 1980-81 observed predation rates and prey selection by the Hornaday River pack (winter), and biomass consumed as per 1977-80 pooled scat data (summer). See Table 56 and text for details.
[3]Based on marrow-fat analysis, where 58% of calves were higher then the mean (81%), and 63% of adults were above the mean (73%).
[4]Population estimates on primary bison ranges.

since winter kills by the Hornaday River pack were felt to be biased toward adult bison in 1978-79, and did not accurately reflect predation patterns over the entire primary bison ranges. The latter figures were arbitrarily based on marrow-fat analysis of bison killed in winter, where 58% of calves killed had fat proportions greater than the mean value of 81% for calves (thus would most likely have survived had they not been killed by wolves), and 63% of adults had fat proportions greater than the mean value of 73% for adult bison. Adult bison losses due to wolf predation thus varied from none when mortality was totally compensatory, to 5.6% when wolf predation by an estimated 136 wolves was totally additive.

The resultant growth potential of the bison population in the absence of wolf predation was calculated from changes in adult and calf losses (Table 64), and showed that when wolf predation was removed, the population increased.

An underlying assumption of this potential population increase was that there were no limits imposed by habitat and available forage, and that wolves played no part in reducing the occurrence of infectious diseases in the park bison population. Caughley (1970, 1976, 1979) considered forage availability in relation to ungulate density as the prime factor in ungulate population regulation and felt that predators were incapable of preventing irruptions of ungulates. Cole (1971) postulated that ungulate populations in the U.S. Rocky Mountain National Parks were regulated by a combination of intraspecific competition and periodic severe weather which affected forage availability. Continuing research on elk in Yellowstone National Park (Houston 1976) hypothesized that predation functioned as a nonessential adjunct to the regulation of population size (Peek 1980).

Contradictory evidence, however, was presented by Bergerud (1974, 1980) which implied that for caribou at least, range deterioration (reduction of forage availability) was not implicated in population declines, and predation (human and natural) was considered the chief limiting factor to population growth. Keith (1974, 1983) held that wolf abundance was primarily determined by the per capita biomass of their ungulate food supply, and wolf predation on ungulates was largely additive to other sources of mortality.

Forage availability on bison ranges in the Slave River lowlands, immediately north of Wood Buffalo National Park was not considered limiting to bison population growth (Reynolds 1974). The dramatic growth of the bison population in the Mackenzie Bison Sanctuary, approximately 100 km northwest of the park, where wolves are also present, suggested that range quality was not a major factor regulating bison populations at current levels in northern Alberta and the Northwest Territories.

No evidence exists at present which links preferential wolf predation with diseased bison in the park, although wolves are known to scavenge diseased carcasses. We do not know to what extent wolf predation may act to suppress, or possibly enhance outbreaks of diseases in bison. We do know that brucellosis has been linked with lowered reproductive potential (Novakowski 1958b, Choquette 1961), and as such its effects may be manifested in the relatively low calf production and annual recruitment of bison observed in the Wood Buffalo National Park area.

It is conceivable that wolves and bison in the park may not have reached an equilibrium until quite recently (i.e. after the massive flood in 1974, and last roundup of bison in 1977); both populations remained

relatively stable throughout the duration of the study. We believe that during 1978-81 the bison population in the primary bison ranges of Wood Buffalo National Park annually lost approximately equal proportions of calves and adults, and recruited yearlings at a rate of about 7.8% (800 bison). We consider that 110 wolves is the best estimate of the number of wolves that were present on the primary bison ranges during the period of study, and these wolves were annually responsible for the death of at least 100 calves and 131 adult bison, the remainder (296 calves and 277 adults) dying of causes other than direct wolf predation. Wolf populations at the time of the study were not as high as in the earlier years (early 1970s). It is conceivable that the overall impact then was considerably higher. As the bison population declines, wolf predation probably will have an increasingly greater impact, until a level of diminishing returns is reached.

Wolves killed approximately 13% (100/750) of calves present in the population in May, whereas 40% (296/750) died from other causes, and wolves killed less than 3% (131/4575) of adult bison, whereas 6% (227/4575) died of other causes. Alternatively wolves were responsible for 25% (100/396) of the annual mortality in calves, and 32% (131/408) of the annual mortality in adult bison. Removal of the effects of wolf predation would result in an increased annual recruitment rate from 7.8% (353/4520) to 9.5% (453/4520), and the adult mortality rate lowered from 8.9% (408/4575) to 6.1% (227/4575), as well as a net annual growth rate from -1.2% (-55/4575) to +3.8% (176/4575).

Success of wolf-removal programs has been reported in other studies (Bergerud 1980, Gasaway et al. 1983) Bergerud documented increased caribou

calf survival after programs of wolf control in Alaska, Northwest Territories and British Columbia. Similarly moose populations in Alaska increased following wolf control programs. In Wood Buffalo National Park we know little of predation by wolves on calves in summer, although our observations of wolf attacks on herds during this time (Oosenbrug et al. 1980a, 1980b; Carbyn et al. 1981) suggested that calves were preferred targets. Calculations of bison killed by wolves showed that although the number of calves and adults killed by wolves was similar (100 to 131), the number of available bison in those age groups was not (750 calves to 4575 adults), indicating an obvious selection for calves.

Selective predation on calves, however, is not in itself proof that wolf predation on calves is largely additive. Bergerud's dismissal (Bergerud 1980) of winter severity as potentially a major mortality factor for caribou calves does not explain the large die offs of both adults and calves documented in the spring and winter 1961/62 (Kelsall 1968). Mortality of moose calves is considerably higher during extreme winters, and is often carried through into the next winter as higher yearling mortality (Peterson 1977). Van Camp (1975) reported that overwinter mortality in a predator-free captive herd of bison was restricted to calves.

In our model, if wolf-predation mortality for calves was indeed totally additive, then removing the source of mortality (wolf predation) would result in a recruitment rate of 11.6% (524/4520) and a net population growth rate of 5.4% (247/4575).

In conclusion, we believe that the bison population in Wood Buffalo National Park during 1978 to 1981 was stationary or declining slightly, and

this trend was primarily due to chronically low production of calves (possibly disease related), and high annual calf losses from unknown sources of mortality, as well as wolf predation. At best, the population has the potential to grow at approximately 9% per year, given the maximum estimated population of wolves (136) be completely removed from the primary bison ranges, and given that mortality from wolf predation is additive and no other factors limit growth in the absence of predation. Given the impracticality of any kind of a wolf-removal program, the unlikelihood that wolves kill bison only in excess of other sources of mortality, and the likely presence of other regulating influences i.e. disease, it seems improbable that the bison population in Wood Buffalo National Park will realize this potential in the near future; rather a continued stabilization or decline seems more likely. It appears from all the data available, low calf production, in the first instance is the most important single factor, currently influencing the status of bison in Wood Buffalo National Park.

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Appendix 1. Capture and monitoring data for wolves collared in Wood Buffalo National Park; February 1978 to June 1981.

Collar no.	Pack affiliation	Sex	Age	Weight (kg)	Colour	Date of capture	Location of capture[4]	No. fixes	No. sightings
U271	Lake Claire	m	ad.	50	Blonde	20/02/78	VA290220	19	11
U270	Lake Claire	m	ad.	43	Grey	20/02/78	VA340160	15	4
U264	Lake Claire	f	imm.	38	Blonde	21/02/78	VA340230	0	0
U273	Lake Claire	m	ad.	52	Grey	22/02/78	VA140030	4	2
U267	Lake Claire	f	imm.	34	Brown	22/02/78	VA140010	2	1
U234	Lake Claire	f	imm.	31	Blonde	23/02/78	VA140040	3	1
281-2[1]	Lake Claire	m	ad.	4[illegible]	Grey	26/01/79	VA190150	18	12
280	Lake Claire	f	ad.	-	Grey	27/01/79	VA135260	3	3
270	Lake Claire	f	imm.	42	Black	28/03/79	VA270095	13	5
274	Lake Claire	f	ad.	-	Blonde	28/03/79	VA230110	4	4
285-6[1]	Lake Claire	f	ad.	43	Grey	28/03/79	VA180080	22	5
272	Lake Claire	m	ad.	54	Blonde	29/03/79	VA170120	14	4
276	Lake Claire	m	ad.	59	Blonde	30/03/79	VA170120	14	3
278	Lake Claire	m	ad.	51	Grey	30/03/79	VA160110	18	3
U265	Hornaday River	f	ad.	41	Blonde	24/02/78	VA580980	0	0
U215	Hornaday River	m	ad.	46	Black	24/02/78	VA590990	13	5
U262	Hornaday River	f	ad.	38	Blonde	06/03/78	VA630820	10	3
269	Hornaday River	f	ad.	34	Blonde	09/01/79	VA575980	61	48
271	Hornaday River	m	ad.	43	Brown	09/01/79	VA570935	61	39
279	Hornaday River	f	imm.	39	Black	19/01/79	VA565850	50	44
275	Hornaday River	m	imm.	50[3]	Black	01/04/79	VA485950	8	5
283-4[1]	Hornaday River	m	ad.	52	Black	01/04/79	VA470955	26	8
346-7[1]	Hornaday River	f	imm.	36	Black	01/12/79	VB495135	189	160
348-9[1]	Hornaday River	f	imm.	37	Black	01/12/79	VB505150	189	166
U263	Willow Point	m	imm.	33	Brown	22/02/78	VV530840	3	3
U268	Welstead Lake	m	ad.	40	Black	22/03/78	VV390650	7	5
U274	Welstead Lake	f	ad.	40	Grey	22/02/78	VV520740	1	0
U261	Darough Creek	m	ad.	46	Black	02/03/78	VA590850	3	2
U272	Darough Creek	f	ad.	39	Black	02/03/78	VA590890	3	3
LC30	Darough Creek	m	ad.	48	Brown	02/03/78	VA580890	2	2
LC38	Murdock Creek	f	imm.	32	Black	07/03/78	VA690550	2	1
U260	Murdock Creek	m	imm.	30	Black	07/03/78	VA670460	4	1
U214	Raup Lake	f	ad.	36	Black	06/03/78	VB490130	3	2
U258	Conibear Lake	f	imm.	30	Grey	23/03/78	VB715095	7	2
U259[2]	Salt River	m	imm.	29	Brown	12/03/78	VB280460	16	4
U275	Salt River	f	ad.	40	Blonde	31/03/78	VB295495	1	0
322	Salt River	m	ad.	54	Grey	18/02/80	VB570120	7	5
323	Salt River	m	ad.	46	Grey	18/02/80	VB570120	78	34
324	Salt River	f	imm.	-	Grey	18/02/80	VB570120	7	5
U280[2]	Rocher River	m	imm.	32	Blonde	06/11/78	VA930105	3	1
273	Baril Lake	m	ad.	58	Black	31/03/79	VA485175	11	2
277	Baril Lake	m	ad.	54	Black	30/03/79	VA480170	12	2
327[2]	Salt River	f	imm.	-	Grey	14/03/81	VB465315	8	2

[1]Double transmitters.
[2]Wolves caught in snares or leg-hold traps.
[3]Wolf gorged with food; 40 kg a more realistic weight.
[4]Universal Transverse Mercator Grid.

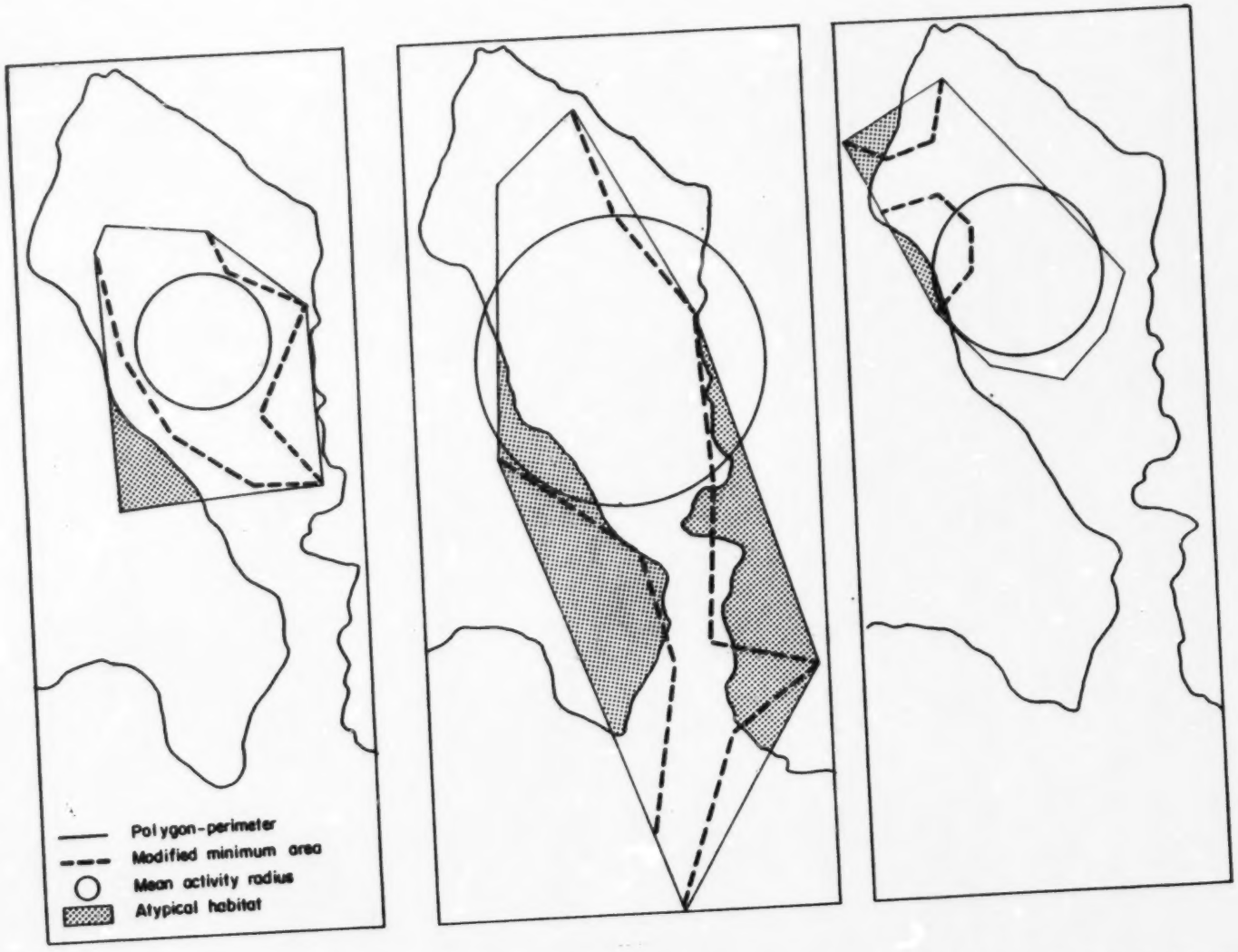
m = male; f = female; ad. = adult; imm. = immature

Appendix 2. Number of packs[1] and wolves identified on primary winter ranges of bison, as determined from aerial bison surveys conducted by Warden Service, Wood Buffalo National Park; 1970-81.

Pack	1970-1	1971-2	1972-3	1973-4	1974-5	1975-6	1976-7	1977-8	1978-9	1979-80	1980-1
Area I											
Hornaday/Darough Ck.	14	19	13	12	14	13	6	13[2]	14[2]	14[2]	10[2]
Murdock Creek	-	8	8	-	-	7	-	10[2]	11[2]	-	-
Salt River/Raup Lake	6	8	-	-	-	-	-	6[2]	5	7[2]	10[2]
Point Providence	-	4	5	-	8	-	8	9	-	8	6
Area II											
Lake Claire	17	15	28	42	12	12	9	14[2]	16[2]	15	10
Hilda Lake	8	17	15	31	-	7	15	5	-	-	
Baril Lake	13	20	30	20	9	13	13	9	8[2]	8	5
Mamawi Lake	-	12	-	-	-	-	-	4[2]	-	9	
Welstead Lake	-	10	8	11	-	-	-	8[2]	-	-	10
Birch River	-	4	18	-	-	-	-	-	-	-	3

[1]Packs defined as groups of three or more wolves.

[2]Pack sizes based on reliable ground observations and radio-telemetric information.



Appendix 3. Calculations of winter home range size of the Hornaday River pack by means of polygon-perimeter, modified, mean activity-radius, and atypical habitat-elimination method on primary bison ranges of Wood Buffalo National Park; 1978-79, 1979-80, and 1980-81.

Appendix 4. Sources of observed and potential mortality in wolves examined in Wood Buffalo National Park, 1978-81.

Date	Age	Sex	Comments
Trapping, snaring and related injuries			
07/03/78	Imm.	Male	Captured by helicopter; recent wounds of body snare
12/03/78	Imm.	Male	Caught alive in body snare; radio collared, released
08/04/78	Adult	Female	Radio collared wolf killed in body snare
06/11/78	Imm.	Male	Caught in leg hold trap; radio collared and released
29/02/80	Adult	Male	Radio collared wolf caught in leg-hold trap; released
07/01/81	Adult	Female	Radio collared wolf killed in body snare
30/01/81	Adult	Male	Radio collared wolf killed in body snare
-/01/81	-	-	Wolf escaped with leg-hold trap (B. Houle, pers. comm.)
06/03/81	-	-	Wolf escaped with leg-hold trap (R. Lewis, pers. comm.)
14/03/81	Imm.	Female	Caught alive in body snare; radio collared, released
05/04/81	Adult	Female	Radio collared wolf killed in body snare
Disease			
20/02/78	Adult	Male	Mange on front and hind legs
02/03/78	Adult	Male	Mange on back and flanks
02/03/78	Adult	Male	Mange localized in pubic area of abdomen
06/03/78	Adult	Female	Mange on shoulders and legs
30/03/79	Adult	Male	Mange on shoulders and rump; died July 1979
31/03/79	Adult	Female	Mange extreme on tail and abdomen
14/03/81	Imm.	Female	Mange on neck and shoulders
Accidents			
07/10/80	Imm.	Female	Hit by vehicle and shot
22/12/80	-	-	Hit and killed by vehicle (D. Anions, pers. comm.)
Intraspecific agression			
--/02/78	Imm.	Female	Killed by other wolves (F. Gibot, pers. comm.)
24/02/80	Imm.	Female	Killed by Hornaday River pack
24/02/80	Adult	Male	Killed by Hornaday River pack
30/03/80	Pup	-	Killed (?) by the Hornaday River pack
Pup mortality			
28/07/78	Pup	-	Died at rendezvous site at Lake One
04/12/78	Pup	Male	Died near Hay Camp

Appendix 5. Mid-month estimates of bison numbers and density[1] on primary winter ranges, as determined from aerial bison surveys, Wood Buffalo National Park; November 1977 to May 1981.

Year	Month	Raup Lake meadows		Hay Camp prairies		Darough Creek prairies		Murdock Creek meadows	
		Numbers	Density	Numbers	Density	Numbers	Density	Numbers	Density
1977	November	8	.025	310	.480	87	.175	196	.485
	December	20	.060	245	.380	67	.135	51	.125
1978	January	7	.020	297	.460	262	.530	235	.580
	February	41	.125	155	.240	379	.765	235	.580
	March	20	.060	174	.270	475	.960	215	.530
	April	7	.020	335	.520	205	.415	83	.205
	May	31	.095	148	.230	257	.520	136	.335
	June	18	.055	48	.075	384	.775	10	.025
	July	50	.155	45	.070	32	.065	2	.005
	August	46	.140	10	.015	0	.000	0	.000
	September	36	.110	100	.155	342	.690	6	.015
	October	62	.190	152	.235	188	.380	6	.015
	November	112	.345	84	.130	111	.225	32	.080
	December	0	.000	61	.095	32	.065	365	.900
1979	January	5	.015	80	.125	37	.075	138	.340
	February	3	.010	123	.190	45	.090	397	.980
	March	0	.000	103	.160	74	.150	464	1.145
	April	15	.045	77	.120	59	.120	90[2]	.223
	May	28	.085	42	.065	40	.080	81[2]	.200
	June	46	.140	10	.015	20	.040	14[2]	.035
	July	163	.500	26	.040	0	.000	9[2]	.023
	August	120	.370	0	.000	47	.095	0	.000
	September	96	.295	181	.280	389	.785	8	.020
	October	78	.240	306	.475	421	.850	65	.160
	November	67	.205	397	.615	173	.350	194	.480
	December	33	.100	210	.325	69	.140	154	.380
1980	January	10	.030	248	.385	109	.220	63	.155
	February	33[2]	.103	290	.450	129	.260	32	.080
	March	33[2]	.103	161	.250	156	.315	43	.105
	April	26[2]	.080	84	.130	334	.675	53	.130
	May	60	.185	10	.015	272	.550	28	.070
	June	47	.145	26	.040	198	.400	18	.045
	July	182	.560	26	.040	99	.200	16	.040
	August	63	.195	55	.085	0	.000	10	.025
	September	73	.225	145	.225	208	.420	6	.015
	October	163	.500	403	.625	216	.435	6	.015
	November	91	.280	158	.245	554	1.120	30	.075
	December	23	.070	123	.190	307	.620	71	.175
1981	January	7	.020	87	.135	210	.425	101	.250
	February	57	.175	87	.135	168	.340	209	.515
	March	81	.250	148	.230	344	.695	200	.495
	April	57	.175	174	.270	260	.525	136	.335
	May	36	.110	126	.195	386	.780	79	.195

[1]Number of bison/km^2.
[2]Figure derived from mean of other years' mid-month estimate.

Appendix 6. Results of aerial bison surveys, and calculated density[1] of bison on primary ranges, Wood Buffalo National Park; November 1977 to June 1981.

Date	Raup Lake meadows		Hay Camp prairies		Darough Creek prairies		Murdock Creek meadows	
	Numbers	Density	Numbers	Density	Numbers	Density	Numbers	Density
15/01/78	5	.015	295	.457	256	.517	240	.593
03/02/78	8	.025	239	.371	419	.846	240	.593
15/02/78	44	.135	142	.220	359	.725	246	.497
15/03/78	17	.052	162	.251	480	.970	213	.430
14/04/78	4	.012	331	.513	206	.416	81	.200
15/05/78	31	.095	145	.225	288	.582	144	.356
15/05/78	18	.055	56	.087	392	.792	9	.022
14/07/78	52	.160	44	.068	1	.002	0	.000
22/08/78	43	.132	1	.002	0	.000	0	.000
15/09/78	34	.105	108	.167	382	.772	5	.012
13/10/78	57	.175	158	.245	195	.394	4	.010
15/11/78	113	.348	8	.126	110	.222	7	.017
18/12/78	0	.000	63	.098	30	.061	366	.904
15/01/79	5	.015	78	.121	38	.077	139	.343
21/02/79	3	.009	130	.202	48	.097	432	1.067
17/03/79	0	.000	107	.166	75	.152	464	1.146
28/06/79	50	.154	0	.000	-	-	-	-
10/07/79	200	.615	30	.047	0	.000	-	-
26/07/79	50	.154	15	.023	0	.000	-	-
14/08/79	120	.369	0	.000	0	.000	-	-
03/10/79	83	.255	268	.416	526	1.063	10	.025
19/11/79	63	.194	451	.659	145	.293	218	.538
22/12/79	-	-	136	.211	41	.083	-	-
30/12/79	18	.055	133	.206	137	.277	-	-
19/01/80	-	-	273	.423	104	.210	-	-
31/01/80	9	.028	339	.526	114	.230	25	.062
10/03/80	-	-	214	.332	150	.303	-	-
16/03/80	-	-	140	.217	171	.345	-	-
21/03/80	-	-	123	.190	224	.453	-	-
25/03/80	-	-	142	.220	440	.889	-	-
01/05/80	2	.006	23	.036	213	.430	59	.146
15/05/80	65	.200	8	.012	285	.576	24	.059
10/07/80	31	.095	33	.051	-	-	-	-
15/07/80	182	.560	22	.034	-	-	-	-
28/07/80	4	.012	-	-	-	-	-	-
13/08/80	62	.191	-	-	1	.002	-	-
26/08/80	70	.215	58	.090	0	.000	-	-
29/08/80	34	.105	2	.003	202	.408	-	-
15/10/80	164	.505	402	.623	216	.436	1	.002
22/11/80	63	.194	150	.233	658	.329	35	.086
19/12/80	-	-	189	.293	293	.592	-	-
23/12/80	5	.015	169	.262	332	.671	82	.202
22/01/81	-	-	144	.223	180	.364	102	.252
02/02/81	4	.012	194	.301	317	.640	-	-
04/02/81	-	-	216	.335	321	.648	-	-
10/02/81	-	-	168	.260	132	.267	-	-
22/02/81	-	-	114	.177	320	.646	-	-
27/02/81	95	.292	197	.305	421	.851	246	.607
13/03/81	-	-	143	.222	351	.709	-	-
23/03/81	-	-	181	.281	231	.467	-	-
30/03/81	-	-	214	.332	273	.552	-	-

Appendix 6. Continued.

Date	Raup Lake meadows		Hay Camp prairies		Darough Creek prairies		Murdock Creek meadows	
	Numbers	Density	Numbers	Density	Numbers	Density	Numbers	Density
09/04/81	-	-	181	.281	223	.451	-	-
22/05/81	29	.089	113	.175	415	.838	-	-
08/06/81	42	.129	32	.050	80	.162	41	.101

[1]Density expressed as bison/km^2, where Raup Lake meadows = 325 km^2
Hay Camp prairies = 645 km^2
Darough Ck. prair. = 495 km^2
Murdock Ck. meadows = 405 km^2

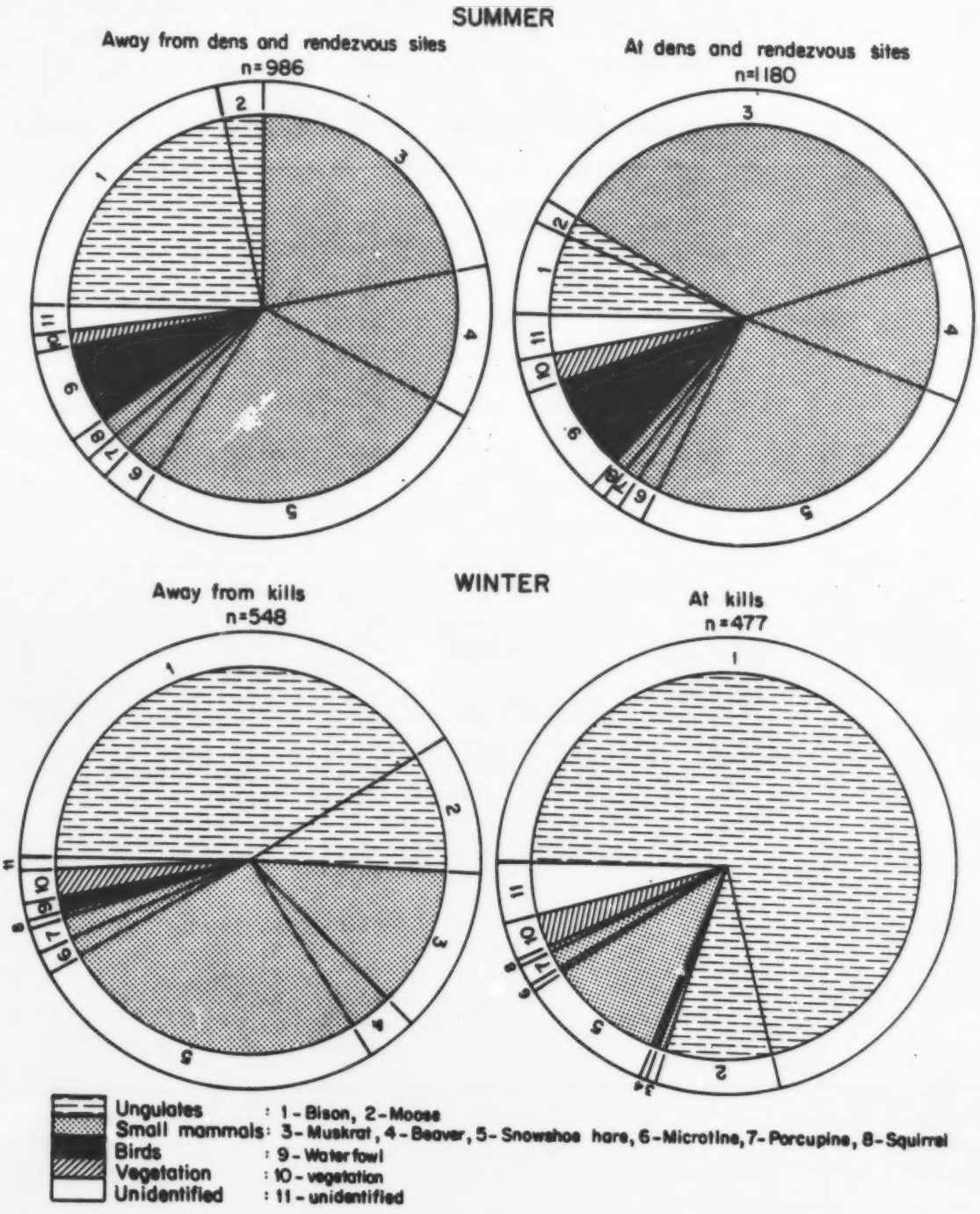
Appendix 7. Age and sex distribution of 131 wolf-killed bison in Wood Buffalo National Park; winters 1971-72 to 1980-81. Figures in brackets are kills made by the Hornaday River pack.

Years	Calves	Yearlings	2-4			5-10			11+			Total
			Males	Females	?	Males	Females	?	Males	Females	?	
Area I												
1971-72 to 1976-77	4	–	–	1	1	3	1	–	2	–	–	12
1977-78	1	2	1	–	–	3	1	–	–	–	–	8
1978-79	–	–	–	–	–	7(7)	4(3)	–	1	2(2)	–	14(12)
1979-80	13(11)	3(3)	–	–	–	2(2)	5(3)	–	2(1)	2(2)	–	27(22)
1980-81	6(6)	–	1	2(1)	–	–	3(2)	–	2(2)	4(3)	–	18(14)
Total	24(17)	5(3)	2	3(1)	1	15(9)	14(8)	–	7(3)	8(7)	–	79(48)
Area II												
1971-72 to 1976-77	1	4	1	–	2	–	2	4	–	–	1	15
1977-78	–	1	–	–	–	1	2	–	1	–	–	5
1978-79	3	–	1	1	–	3	1	–	1	–	–	9
1979-80	–	–	–	–	–	1	3	–	–	1	–	5
1980-81	3	–	–	2	1	6	4	–	1	1	–	18
Total	7	5	2	3	3	11	12	4	2	2	1	52
Combined areas												
1971-72 to 1976-77	5	4	1	1	3	3	3	4	2	–	1	27
1977-78	1	3	1	–	–	4	3	–	1	–	–	13
1978-79	3	–	1	1	–	10	5	–	1	2	–	23
1979-80	13	3	–	–	–	3	8	–	2	3	–	32
1980-81	9	–	1	4	1	6	7	–	3	5	–	36
Total	31	10	4	6	4	26	26	4	9	10	1	131

Appendix 8. Percent marrow fat distribution in 72 wolf-killed bison; Wood Buffalo National Park, 1977-78 to 1980-81.

Years	Calves	Yearlings	2-4 Males	2-4 Females	5-10 Males	5-10 Females	11+ Males	11+ Females
Area I								
1977-78			76.5[1]		76.1[2]			
					95.4[2]			
					9.6[3]			
1978-79					78.2[1]	80.7[2]	73.6[3]	71.8[3]
					98.5[2]	84.5[3]		62.4[3]
					38.9[2]			
					54.3[2]			
					83.4[3]			
					38.0[3]			
1979-80	88.8[1]	82.0[1]			80.2[3]	69.6[1]	59.8[2]	86.4[1]
	85.5[2]	91.3[1]				88.3[1]	69.9[3]	70.4[2]
	98.2[2]	67.9[2]				49.6[2]		
	89.9[2]					38.6[3]		
	72.6[2]					79.4[3]		
	77.2[3]							
	78.6[3]							
1980-81	83.3[3]			88.8[3]		88.4[1]	6.7[3]	55.0[1]
				83.0[3]		75.0[2]		72.9[2]
						88.7[2]		81.3[2]
								95.4[3]
Area II								
1977-78					61.6[1]	94.4[1]	82.4[2]	
						77.7[2]		
						63.5[2]		
1978-79	63.0[3]		79.5[1]	37.1[3]	73.4[2]	58.7[2]		
	81.6[3]				86.8[3]			
	84.5[3]							
1979-80					65.0[2]	94.3[2]		
						82.9[2]		
						85.0[3]		
1980-81	65.6[2]			84.0[2]	90.0[1]	88.5[2]	31.5[2]	
				83.5[3]	86.7[2]	73.9[3]		
					82.8[3]			

[1]Early winter.
[2]Midwinter.
[3]Late winter.


SUMMER
Away from dens and rendezvous sites
n=986
At dens and rendezvous sites
n=1180
WINTER
Away from kills
n=548
At kills
n=477
Ungulates : 1 - Bison, 2 - Moose
Small mammals: 3 - Muskrat, 4 - Beaver, 5 - Snowshoe hare, 6 - Microtine, 7 - Porcupine, 8 - Squirrel
Birds : 9 - Waterfowl
Vegetation : 10 - vegetation
Unidentified : 11 - unidentified

Appendix 9. Percent frequency occurrence of food items in scats collected in summer (May to October) and winter (November to April) from 1977 to 1980 in Wood Buffalo National Park.

Appendix 10. Results of midwinter total counts on primary bison ranges of Wood Buffalo National Park, 1978-79 to 1980-81.

	1978-79	1979-80	1980-81
Area I			
Raup Lake meadows	3	9	95 (3)
Hay Camp meadows	131 (5)[1]	339 (26)	197 (13)
Darough Creek meadows	48	114 (4)	421 (41)
Murdock Creek meadows	432	25	246 (27)
Others	213	206 (13)	239 (19)
Total	826	693 (43)	1198 (103)
Area II			
All primary ranges	3631	3450	3503 (361)
Park total	4457	4143	4701

[1]Calf numbers, where available, are shown in brackets.

Appendix 11. Summary of bison population trend from 1978 to 1981 on the primary bison ranges of Wood Buffalo National Park, with best fit to observed calf proportions and total estimated bison recorded on annual midwinter aerial surveys.[1]

Data input			Adults	Calves	Population size
Total count (1978)[3]					4685
Calf proportion:	May	(14.7%)	4685	807(+807)	5492
	August	(14.7%)	4685	807	5492
Adult mortality:	May-Oct.	(2.5%)	4568(-117)	807	5375
Calf proportion:	November	(10.6%)	4568	542(-265)	5110
Adult mortality:	Nov.-Feb.	(5.0%)	4340(-228)	542	4882
Calf proportion:	February	(10.6%)	4340	515(-27)	4855
Total count (1979)[3]					4457
Adult mortality:	Mar.-Apr.	(5.0%)	4123(-217)	515	4638
Calf proportion:	April	(9.7%)[4]	4123	443(-72)	4565
Estimated bison population (30 April 1979)					4565
Calf proportion:	May	-	4575	-	4565
	August	(10.1%)	4565	513(+513)	5078
Adult mortality:	May-Oct.	(2.5%)	4451(-114)	513	4964
Calf proportion:	November	(8.8%)	4451	429(-84)	4880
Adult mortality:	Nov.-Feb.	(2.5%)	4340(-111)	429	4769
Calf proportion:	February	(6.1%)	4340	282(-147)	4622
Total count (1980)[3]					4143
Adult mortality:	Mar.-Apr.	(2.5%)	4232(-108)	282	4514
Calf proportion:	April	(5.4%)	4232	242(-40)	4474
Estimated bison population (30 April 1980)					4474
Calf proportion:	May	(17.2%)	4474	929(+929)	5403
	August	(15.5%)	4474	821(-108)	5295
Adult mortality:	May-Oct.	(2.5%)	4362(-112)	821	5183
Calf proportion:	November	(12.1%)	4362	600(-221)	4962
Adult mortality:	Nov.-Feb.	(2.5%)	4253(-109)	600	4853
Calf proportion:	February	(9.9%)	4253	467(-133)	4720
Total count (1981)[3]					4701
Adult mortality:	Mar.-Apr.	(2.5%)	4147(-106)	467	4614
Calf proportion:	April	(8.3%)[4]	4147	375(-92)	4522
Estimated bison population (30 April 1981)					4522

[1]Assume annual adult mortaility as 12.5% in 1978-79, and 7.5% in 1979-80 and 1980-81.
[2]Bison older than one year.
[3]Estimated total bison numbers based on annual midwinter total count survey.
[4]Extrapolated decrease in calf proportions, based on May-February monthly mean decrease = recruitment (new-yearling proportion).